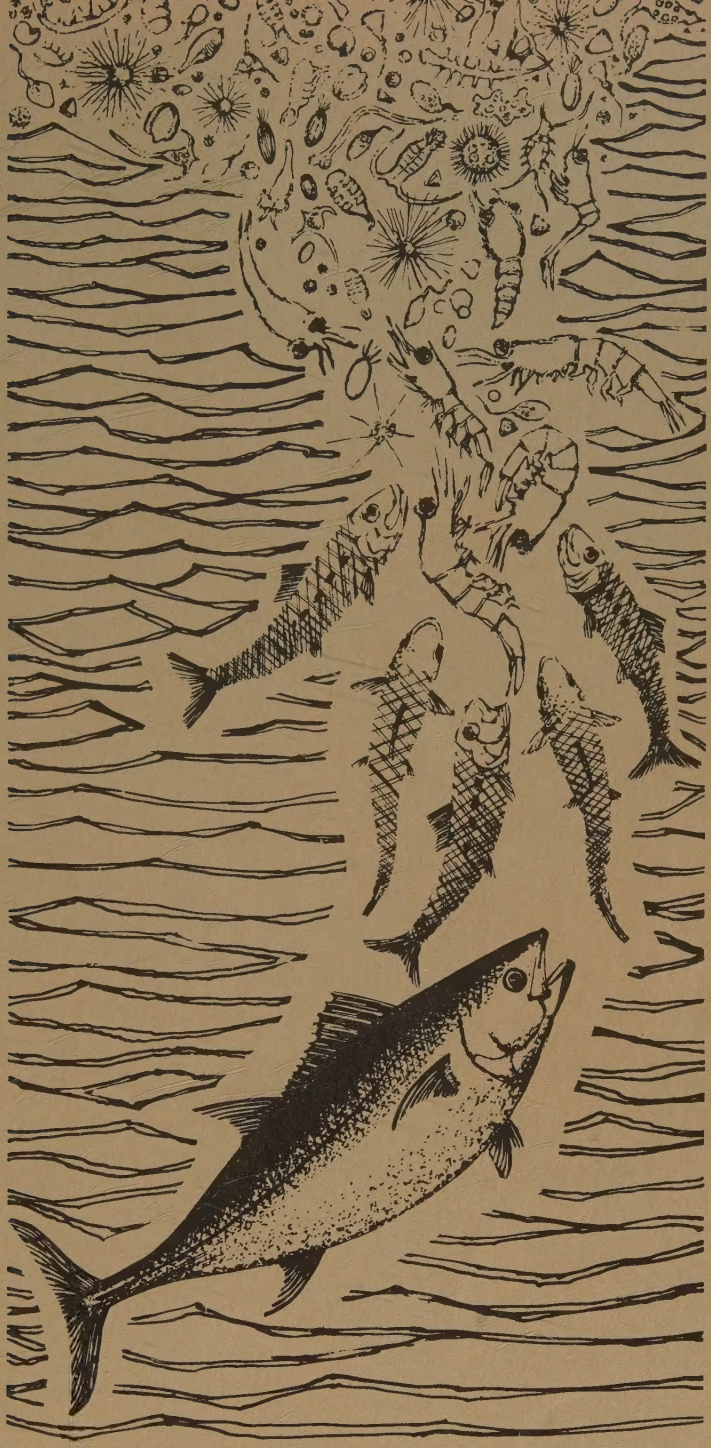

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Created in 1849, the U.S. Department of the Interior is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

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DISTRIBUTION OF LARVAL TUNAS IN MARQUESAN WATERS

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ABSTRACT

Spawning of tunas near the Marquesas Islands was investigated by studying the distribution of larval tunas collected in 1957 and 1958. Of the six species of larval tunas identified, larval skipjack (*Katsuwonus pelamis*) occurred most frequently. Prominent diel variation with greater catches at night was observed at a station occupied for 24 hours in December 1957 and March 1958 for larval skipjack and in January 1958 for larval yellowfin (*Thunnus albacares*). Both the incidence of the capture of larval tunas and their abundance were greater during the southern summer and fall (January to April) than in the other months of the year. There was no difference in abundance of larval tunas with respect to distance from shore, nor were there any differences in abundance among the four transects (north, east, south, and west of the islands) along which sampling was conducted. No significant correlation was found between abundance of invertebrate plankton and larval tunas nor between schools of adult tunas sighted and abundance of larval tunas. Temporal distribution of larvae indicated some spawning by skipjack throughout the year.

Oceanographic and fishing surveys in the Pacific near the Marquesas Islands (fig. 1) during 1957–58 were part of a program undertaken by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, to investigate the tuna resources in this area. Pertinent to this investigation was a study of the time and location of the spawning of tunas.

Methods of determining spawning activities of tunas involve inferences from studies of their ovaries and the distribution of their larvae. The latter method has been made possible by the identification (tentative for some species) and detailed descriptions of the larvae of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), bigeye (*Thunnus obesus*), albacore (*Thunnus alalunga*), bluefin (*Thunnus thynnus orientalis*), longfin (*Thunnus tonggol*), three species of *Euthynnus*, and *Auxis* sp. (Matsumoto, 1958, 1959, 1962; Mead, 1951; Wade, 1951). Attempts to identify specifically eggs of these tunas have been unsuccessful because of their similarity

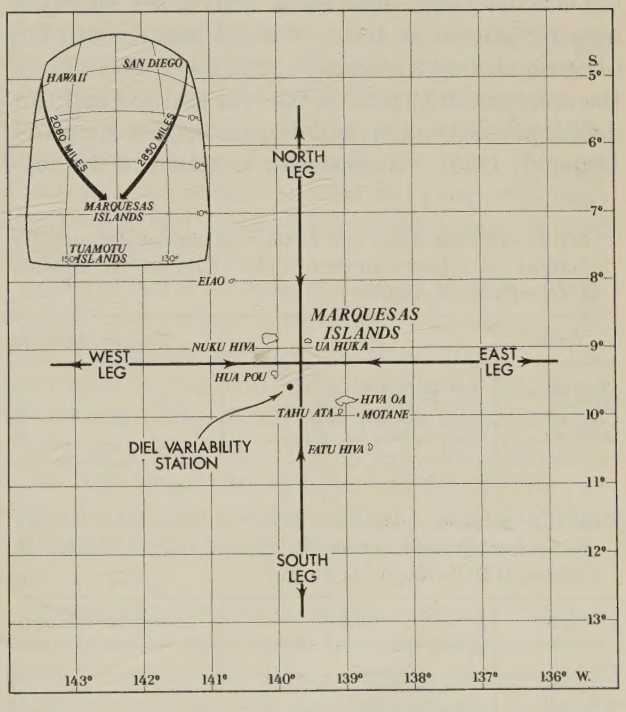

FIGURE 1.—Offshore survey track and the diel variability station in the Marquesas, 1957–58.

NOTE.—Approved for publication October 12, 1965.

in appearance and the overlapping ranges of their diameters (Matsumoto, 1958).

This report presents information on the abundance and distribution of larval tunas in the region of the Marquesas Islands. Six species of larval tunas were identified, but emphasis is on skipjack, as it occurred more often than the others. Inferences concerning skipjack spawning are compared with those derived from ovarian studies of this species from the same area (Yoshida, 1965).

COLLECTION OF SAMPLES

Plankton samples from which the larval tunas were sorted and counted were collected from research vessels of the Bureau of Commercial Fisheries in 1957 and 1958 on a standardized offshore survey pattern and at a diel variability station (fig. 1). The latter was situated at lat. 9°34′ S. and long. 139°50′ W. (about 15 miles southeast of the island of Hua Pou) and was occupied for 24-hour periods on six occasions. Cruises, dates, and numbers of samples obtained on the offshore surveys and at the diel variability station are summarized in tables 1 and 2 respectively. Fishery and environmental data collected on these cruises have been published by Wilson, Nakamura, and Yoshida (1958).

Plankton hauls were made with a net having a mouth diameter of 1 m. The net was constructed of nylon netting with mesh apertures of 0.66 mm. in the body and 0.31 mm. in the rear and cod end (for details of construction and dimensions, see King and Demond, 1953). A flowmeter mounted in the center of the mouth provided estimates of the amount of water strained.

Oblique, open-net, ½-hour plankton hauls from the surface down to 140 m. and back to the surface were taken during the offshore surveys and at the diel variability station on all cruises. A second net was attached to the towing cable to permit sampling between 140 and 280 m. at the diel variability station on *Hugh M. Smith* cruise 45 (HMS–45). This latter net was similar to the open one but was modified to permit attachment of opening and closing devices (King, Austin, and Doty, 1957).

Two consecutive ½-hour tows were made during *Charles H. Gilbert* cruise 35 (CHG–35) to obtain data for testing the duplicability of the catches.

On the offshore surveys, plankton hauls were made twice each night, once before midnight (between 2000 and 0000 hours) and once after midnight (between 0200 and 0400 hours). At the diel variability station, duplicate hauls were made every 3 hours on CHG–35, while single hauls were taken at 2-hour intervals on the other cruises.

Plankton samples were preserved in 10 percent Formalin.[1]

In the laboratory all fish and fish eggs were sorted from plankton samples with the aid of binocular dissecting microscopes. From these collections of fish and eggs, larval tunas were separated and identified. Most of the larvae were less than 5 mm. in total length. Specimens greater than 10 mm. comprised a very small percentage of the total number.

TABLE 1.—*Cruises, dates, and numbers of zooplankton samples obtained on offshore surveys* [*CHG* = Charles H. Gilbert, *HMS* = Hugh M. Smith]

Cruise	Dates	Number of samples
CHG–35	Oct. 24–Nov. 7, 1957	46
HMS–43	Jan. 27–Feb. 12, 1958	22
CHG–38	Mar. 26–Apr. 9, 1958	24
HMS–45	May 15–May 30, 1958	21

TABLE 2.—*Cruises, dates, and numbers of zooplankton samples obtained at the diel variability station* [*CHG* = Charles H. Gilbert, *HMS* = Hugh M. Smith]

Cruise	Dates	Number of samples
CHG–35	Oct. 21–22, 1957	16
CHG–35	Dec. 1–2, 1957	16
HMS–43	Jan. 23–24, 1958	12
CHG–38	Mar. 6–7, 1958	12
CHG–38	Apr. 17–18, 1958	12
HMS–45	June 8–9, 1958	24

TREATMENT OF DATA

Larval abundance is expressed as the number of larvae in a column of water 10 m. square and 140 m. deep. This value was obtained by multiplying the number of larvae per cubic meter of water strained by the volume of the column of water.

Nonparametric statistics (Siegel, 1956) were used in our analyses to avoid assumptions of normal distributions.

Data on plankton hauls and numbers of larval tunas collected at the diel variability station and on the offshore surveys are presented in appendix tables A–1 through A–8.

DUPLICABILITY OF CATCHES

Catches of larval tunas by successive tows were compared by Strasburg (1960). He found no sig-

[1] Trade names referred to in this publication do not imply endorsement of commercial products.

nificant difference and concluded that plankton nets were reliable tools for sampling larval tunas within the limitations of the method. All of his tows were taken at the surface and at night.

To determine if catches could be duplicated during other hours and with oblique tows, the data from the 39 pairs of plankton tows taken during CHG–35 were examined. The abundance of larval tunas calculated from catches of the first tow did not differ significantly (Wilcoxon matched-pairs signed-ranks test) from that of the second. We thus concluded that catches by oblique tows taken during day or night were duplicative.

SPECIES COMPOSITION

Larvae of the following species of tunas were identified in the Marquesan samples: skipjack, yellowfin, bigeye, albacore, little tunny (*Euthynnus affinis*), and frigate mackerel (*Auxis* sp.)[2]. Adults of all except *Auxis* have been caught either by longline, trolling, or pole-and-line fishing in the Marquesas (King et al., 1957; Austin, 1957; Wilson and Rinkel, 1957; Wilson et al., 1958; Yoshida, 1960). Another species, the dogtooth tuna (*Gymnosarda nuda*), also has been caught in the Marquesas by trolling near the islands, but its larva has not been identified.

The species composition of the larval tunas is shown in table 3. Skipjack was the dominant species throughout the offshore surveys and at all but one of the diel variability stations. At the diel variability station occupied during HMS–43, yellowfin was dominant (appendix table A–2). Other species were found in sporadic abundance, e.g., *Auxis* at the second diel variability station of CHG–35 (appendix table A–1), bigeye at the diel variability station of HMS–43 (appendix table A–2) and on the offshore surveys of CHG–38 (appendix table A–7) and HMS–45 (appendix table A–8).

TABLE 3.—*Species composition of larval tunas collected in Marquesan waters, 1957–58*

Species	Diel variability station		Offshore surveys	
	Number collected	Percent of total catch	Number collected	Percent of total catch
K. pelamis	351	63.8	472	83.0
T. albacares	63	11.5	19	3.3
T. obesus	30	5.5	41	7.2
T. alalunga	3	0.5	8	1.4
E. affinis	2	0.4	0	0
Auxis sp.	80	14.5	10	1.8
Unidentified tuna	21	3.8	19	3.3
Total	550		569	

[2] May include both *A. thazard* and *A. rochei* (=*A. thynnoides*); see Matsumoto (1959).

DIEL AND SEASONAL DISTRIBUTION

Diel variation in catches of larval tunas has been discussed by Wade (1951), Matsumoto (1958), and Strasburg (1960). All reported greater catches at night. The latter two authors attributed this primarily to vertical migration by the larvae into the upper surface layers of the ocean at night, although they did not rule out the possibility of net dodging during daylight.

Since Strasburg (1960) found practically no larval tunas below 140 m., our sampling did not extend below this depth (except at the diel variability station on HMS–45). By sampling the 0- to 140-m. depth range, we hoped that variations due to diel vertical migration would be kept to a minimum or even possibly eliminated.

Catches at the diel variability station during CHG–35, HMS–43, and CHG–38 provided evidence that this variation was not eliminated. Prominent diel variations occurred in December and March for skipjack and in January for yellowfin (fig. 2). Either the larvae did occur below 140 m., or they were more successful in escaping the net during the day in these instances. The problem of diel variation was complicated further by the inconsistency of the catches during the other months. For example, the highest catches of larval skipjack were obtained during or near twilight in April and June, while during October and January day catches were as good as night catches.

Average larval abundance during the offshore surveys of each cruise was compared with those of the other cruises for seasonal variation (fig. 3). The abundance during HMS–43 (January to February) and during CHG–38 (March to April) was significantly greater (Mann–Whitney U test, $p<0.05$) on both occasions than for either HMS–45 (May) or CHG–35 (October to November). No significant differences were found in other comparisons of offshore averages.

Averages for the diel variability station, computed from results of tows taken between 2000 and 0400 hours, the same hours during which tows were taken on the offshore surveys, also are shown in figure 3. The magnitudes and variations of these averages differ considerably from those of the offshore surveys.

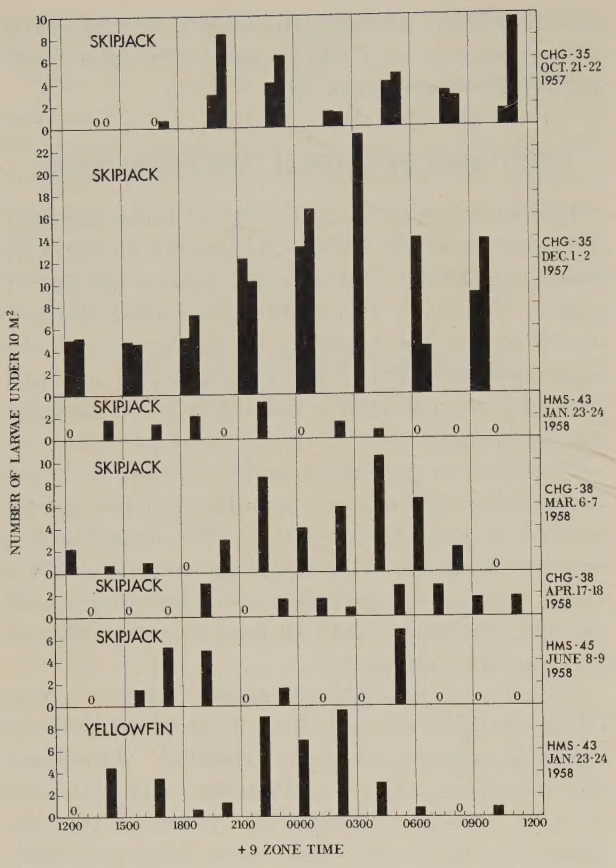

FIGURE 2.—Diel variation in abundance of larval skipjack and larval yellowfin.

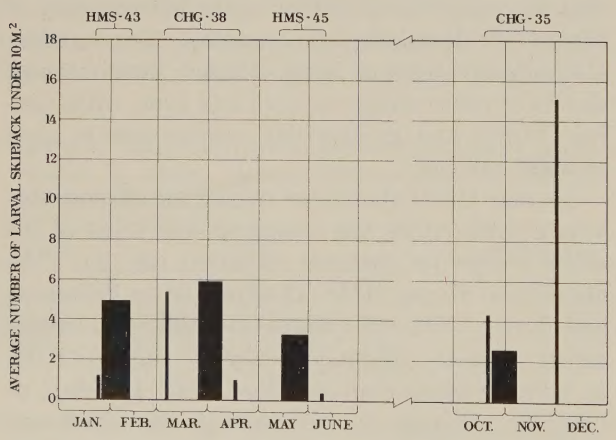

FIGURE 3.—Seasonal variation in the abundance of larval skipjack. The slender bars represent averages for the diel variability station, the thick bars averages for the offshore surveys.

The averages for the offshore surveys represent more samples and a greater areal and temporal coverage than those for the diel variability station. Based on the offshore data, skipjack spawning appears to be greater during the southern summer (January to February) and early fall (March to April), but paucity of data during the southern winter and spring (June to October) makes this conclusion tenuous.

VERTICAL AND HORIZONTAL DISTRIBUTION

Strasburg (1960) observed that most larval tunas were captured within the upper 60 m. of water, with 20 to 25 percent of the catch within the 70- to 130-m. depth, and practically none below 140 m. Since the possibility of larval tunas in waters below 140 m. had been indicated in the earlier cruises (fig. 2), special plankton hauls were planned for the diel variability station during HMS–45. A closing net of dimensions similar to those of the open net was added to the towing cable to permit sampling at depths between 140 and 280 m. Although simultaneous sampling was planned for depth ranges of 0 to 140 and 140 to 280 m., the actual maximum depth sampled by the upper net ranged between 121 and 150 m., while the depths sampled by the lower net ranged between 70 and 262 m. (appendix table A–4).

No larval tunas were caught by the lower net. Larvae were caught only in 6 of the 12 hauls by the upper net. Although the results did not conflict with those of Strasburg, the meager catches and the departures from the planned sampling depths caused the results to be inconclusive.

A relation between larval skipjack distribution and area was not evident. No significant areal association (Kendall coefficient of concordance) was found in the average abundance of larvae for the several legs of the offshore survey track, nor was a relation between larval distribution and proximity to land found in a comparison (Kendall coefficient of concordance) of the average abundance by inner, middle, and outer 75-mile sections of the offshore survey legs (tables 4 and 5).

TABLE 4.—*Average number of larval skipjack under 10 m.² of ocean surface for the north, south, east, and west legs of the offshore surveys (fig. 1).*

[Numbers of samples on which the averages are based are in parentheses]

Cruise	North leg	South leg	East leg	West leg
CHG-35	2.5 (12)	3.3 (10)	0.9 (12)	3.9 (12)
HMS-43	5.9 (6)	5.6 (6)	4.4 (4)	3.6 (6)
CHG-38	11.4 (6)	4.2 (6)	4.0 (6)	3.9 (6)
HMS-45	1.2 (5)	2.5 (6)	8.8 (5)	0.9 (5)

TABLE 5.—*Average number of larval skipjack under 10 m.² of ocean surface for the inner, middle, and outer 75-mile sections of the offshore surveys.*

[Numbers of samples on which the averages are based are in parentheses]

Cruise	Inner 75 miles		Middle 75 miles		Outer 75 miles	
CHG-35	2.3	(14)	2.7	(16)	2.9	(16)
HMS-43	1.9	(8)	6.1	(6)	7.1	(8)
CHG-38	6.2	(8)	5.7	(8)	5.7	(8)
HMS-45	3.2	(5)	4.8	(8)	1.9	(8)

Larval skipjack had been found to be widely distributed in the northeastern part of French Oceania previous to the series of cruises in this report. Figure 4 illustrates the locations around the Marquesas

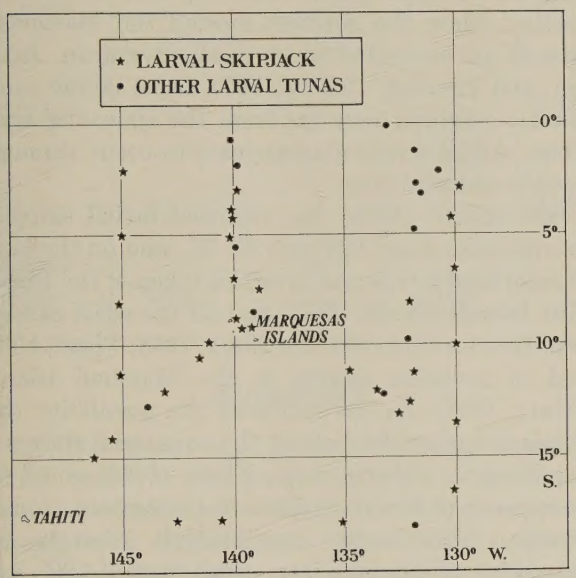

FIGURE 4.—Stations in northeastern French Oceania where larval tunas were collected on cruises earlier (1952–57) than those covered by this study. (Data from Matsumoto, 1958, and Strasburg, 1960.)

Islands where larval tunas were collected during cruises of vessels of the Bureau of Commercial Fisheries prior to those listed in table 1.

ABUNDANCE OF LARVAL TUNAS AND INVERTEBRATE PLANKTON

Relations between the abundance and distribution of invertebrate plankton and of larval tunas, if any exist, are obscure. If the plankton volumes and abundance of larval tunas are averaged for each of the offshore surveys, an obvious positive correlation

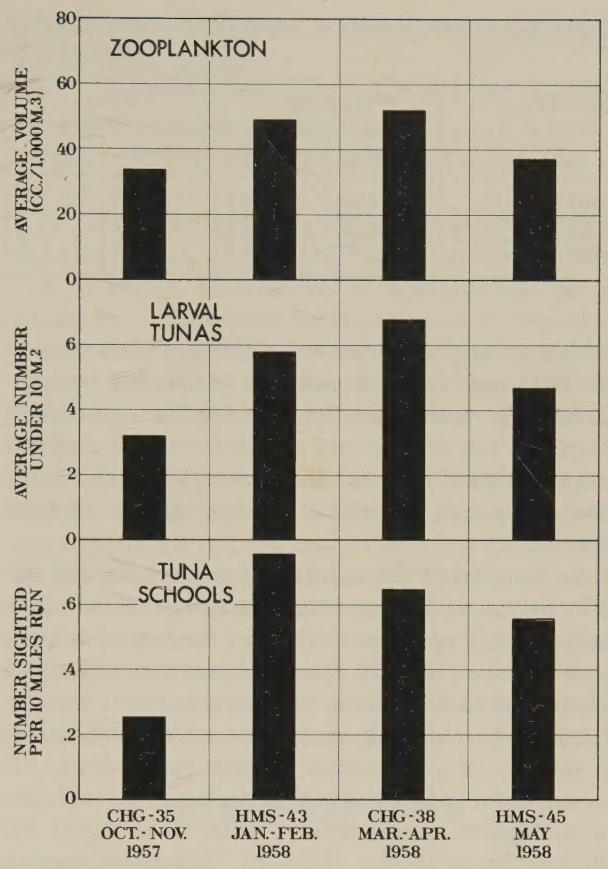

FIGURE 5.—Average abundance of zooplankton, larval tunas, and tuna schools for the offshore surveys.

can be seen (fig. 5), but in individual samples no significant correlations (Spearman rank correlation) were found. High and low measures of abundance of larval tunas were found in high as well as in low volumes of plankton. Strasburg (1960) reported that high catches of larval tunas came from samples of low and moderate volumes of plankton, while the samples with lowest and highest plankton volumes contained smaller numbers of larval tunas.

ABUNDANCE OF LARVAL AND ADULT TUNAS

Strasburg (1960) found a tendency for larval tunas to occur in larger abundance where there were more adults of the same species although the correlation was statistically nonsignificant. Similar comparisons by species were not possible with our data. Schools of adult tunas were located by sighting the associated bird flocks. Because of the necessity of covering a certain distance of the offshore surveys

TABLE 6.—*Average number of larval tunas under 10 m.² of ocean surface and number of schools sighted per 10-mile run for the legs of the offshore surveys*

Cruise	North leg		East leg		South leg		West leg		Entire survey	
	Schools	Larvae	Schools	Larvae	Schools	Larvae	Schools	Larvae	Schools	Larvae
CHG–35	0.405	3.2	0.183	1.8	0.207	3.4	0.226	4.3	0.256	3.2
HMS–43	1.020	7.2	.884	5.4	.569	6.8	.560	3.6	.758	5.8
CHG–38	.909	14.6	.390	4.4	.591	4.3	.708	3.9	.649	6.8
HMS–45	.591	3.9	.275	9.4	1.013	2.9	.380	2.9	.559	4.7

within an allotted time, investigation of schools was discontinued if the response to chumming was unfavorable. Consequently, the specific identity of many of the schools was not determined, and our examination of the relation between larval and adult abundance was in terms of the aggregate of all tuna species.

In comparing the number of schools sighted per 10-mile run and the average number of larval tunas under 10 m.² of ocean surface for the legs of the offshore surveys and for the inner, middle, and outer 75-mile sections of these legs, no significant correlations (Spearman rank correlation) were found (tables 6 and 7). For the entire offshore survey area, the averages for both adult tuna schools and larval tunas were highest during either HMS–43 or CHG–38, slightly lower during HMS–45, and lowest during CHG–35. A similar pattern was found in the average of zooplankton volumes. The variations of all three averages are illustrated in figure 5.

TABLE 7.—*Average number of larval tunas under 10 m.² of ocean surface and number of schools sighted per 10-mile run for 75-mile sections of the legs of the offshore surveys*

Cruise	Inner 75 miles		Middle 75 miles		Outer 75 miles	
	Schools	Larvae	Schools	Larvae	Schools	Larvae
CHG–35	0.452	2.8	0.305	3.0	0.030	3.7
HMS–43	.867	3.0	.554	7.4	.833	7.3
CHG–38	1.145	6.8	.460	7.1	.393	6.5
HMS–45	.412	3.8	.586	6.0	.695	3.9

INFERENCES CONCERNING SKIPJACK SPAWNING

Inferences about spawning based on the size of the larva upon hatching have been discussed by Matsumoto (1958). He hypothesized that skipjack are 2.5 mm. or less at hatching, that the eggs and larvae are planktonic and therefore subject to dispersion by currents, but that their displacement from the spawning site would be relatively insignificant unless the currents were exceptionally strong. Larval skipjack have been taken throughout the area around the Marquesas Islands (fig. 4). Most of the catch consisted of larvae between 3 and 4.5 mm. long, so we may assume that they had hatched recently. Since the currents around the Marquesas Islands are suspected to be weak (Sverdrup, Johnson, and Fleming, 1942: p. 702), these larvae could not have drifted very far from the spawning sites. Thus, skipjack spawning appears to occur throughout the sampled area.

Matsumoto (1958) has reported larval skipjack catches from long. 180° to 120° W., and on the basis of records of larvae and juveniles taken in the Philippine Islands (Wade, 1951) and off the coast of Central America (Schaefer and Marr, 1948; Mead, 1951) and of juveniles caught in the Marshall Islands (Marr, 1948), he has indicated the possibility that skipjack spawn throughout the equatorial waters of the Pacific. Subsequently, Klawe (1963) noted the occurrence of larval skipjack in the eastern tropical Pacific. Matsumoto (unpublished) recently obtained larval skipjack from areas west of 180°, particularly around the Marshall Islands and the eastern part of the Caroline Islands. Capture of larval skipjack in localities still farther west in the Marianas and Palau Islands was reported by Yabe, Yabuta, and Ueyanagi (1963). These records confirm Matsumoto's hypothesis of the transoceanic distribution of larval skipjack in the Pacific.

Matsumoto (1958) also has reported the north-south distribution of larval skipjack as extending from lat. 25° N., to 14½° S. in the central Pacific. The southern limit now may be extended to at least lat. 18° S.

Table 8 shows the months during which larval skipjack have been taken in northeastern French Oceania on various cruises by vessels of the Bureau of Commercial Fisheries. They were captured in all months except July, in which no sampling was

done. Thus, skipjack spawning can be inferred to occur throughout the year in these waters. Yoshida (1965) likewise concluded from a study of skipjack ovaries that skipjack spawn year-round in the Marquesas.

Yoshida also concluded that spawning is greatest from November through April. Although the seasonal distribution of larval skipjack (fig. 3) is consistent with Yoshida's results, the data do not permit a comparison for all seasons.

TABLE 8.—*Months, years, and cruises during which larval skipjack have been captured in northeastern French Oceania. Italicized cruises sampled the Marquesan offshore survey area.*

[Data prior to October 1957 from Matsumoto (1958) and Strasburg (1960)]

Month	Year			
	1952	1956	1957	1958
January				*HMS–43*
February			HMS–38 *CHG–32*	*HMS–43*
March		HMS–33	HMS–38 *CHG–32*	*CHG–38*
April				*CHG–38*
May				*HMS–45*
June	*HMS–15*			*HMS–45*
July				
August		CHG–30		
September		*CHG–30*		
October			*CHG–35*	
November	HMS–18		*CHG–35*	
December			*CHG–35*	

SUMMARY

1. The results of a study of the distribution of larval tunas in Marquesan waters are presented. Data were collected in 1957 and 1958 on repeated transits of a standardized offshore survey pattern and on repeated visits to a single station where diel variability of larval abundance was studied.

2. Larval tunas were sorted and counted from 113 plankton samples from the offshore surveys and 92 from the diel variability station. Larval abundance is expressed as the number of larvae under 10 m.^{2} of ocean surface down to a depth of 140 m.

3. Duplicability of larval catches by oblique tows taken at night or day was demonstrated.

4. Greater abundance of larval skipjack during darkness was evident at the diel variability station in December 1957 and March 1958 and of larval yellowfin in January 1958. Greater abundance of larval skipjack at twilight was found in April and June of 1958. Results of attempts to determine whether larvae were below 140 m. were inconclusive.

5. Data from the offshore surveys indicate greater abundance of larval tunas during the Marquesan summer and fall (January to April) than during other months.

6. Larval skipjack have been collected throughout the area of northeastern French Oceania bounded by long. 130° W. and 147° W. from the Equator to lat. 18° S.

7. High and low catches of larvae occurred in samples of high as well as of low plankton volume.

8. Average abundances of zooplankton, larval tunas, and tuna schools for the offshore surveys were lowest during CHG–35 (Oct.–Nov. 1957), highest during either HMS–43 (Jan.–Feb. 1958) or CHG–38 (Mar.–Apr. 1958), and intermediate during HMS–45 (May 1958).

9. According to records of the localities of the capture of larvae and juveniles, skipjack spawn throughout the tropical and subtropical zones of the Pacific Ocean. In northeastern French Oceania, skipjack appear to spawn throughout the year. The data are consistent with the conclusion reached from a study of skipjack ovaries that the spawning of skipjack in northeastern French Oceania is most active from November through April.

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APPENDIX

TABLE A–1.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′W.) on* Charles H. Gilbert *cruise 35*

Station	Date (1957)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	*M.*³	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
18	Oct. 21	0739–0811	0–140	2185.1	5							5
19	do	0814–0845	0–140	2112.5	4						1	5
20	do	1035–1105	0–140	1927.0	2			1(?)			3	6
21	do	1108–1137	0–140	1895.9	13		4(?)					17
22	do	1335–1405	0–140	1789.0								0
23	do	1406–1434	0–140	1860.8								0
24	do	1632–1703	0–140	2082.5								0
25	do	1706–1737	0–140	2068.2	1							1
26	do	1933–2005	0–140	2331.2	5	1					4	10
27	do	2007–2037	0–140	1842.2	11							11
28	do	2235–2305	0–140	1735.6	5							5
29	do	2306–2338	0–143	1979.1	9		1					10
30	Oct. 22	0143–0213	0–140	2039.6	2						1	3
31	do	0214–0244	0–140	2078.5	2	1						3
32	do	0431–0459	0–140	1733.9	5	1						6
33	do	0501–0532	0–140	2073.1	7							7
119	Dec. 1	0608–0638	0–140	1705.9	17							17
120	do	0639–0711	0–143	1936.4	6							6
121	do	0905–0936	0–140	1709.6	11						1	12
122	do	0939–1008	0–140	1917.3	19					1		20
123	do	1205–1237	0–140	1681.6	6							6
124	do	1239–1310	0–140	1599.5	6					2	2	10
125	do	1506–1537	0–142	1765.8	6		1					7
126	do	1539–16 0	0–142	1809.0	6				1		2	9
127	do	1805–1835	0–140	1361.9	5							5
128	do	1836–1907	0–140	1352.2	7							7
129	do	2103–2133	0–140	1375.9	12					1	1	14
130	do	2134–2006	0–140	1503.4	11		1			5		17
131	Dec. 2	0005–0035	0–140	1481.8	14		2	1(?)		13		30
132	do	0037–0106	0–140	1516.9	18		2(?)	1(?)	1	23	4	49
133	do	0304–0334	0–140	1564.6	26					30		56
134[2]	do	0336–0405	0–140	1649.7	8							8

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

[2] Sample considered atypical because salps comprised 95 percent (estimated) of the volume and 71 percent (estimated) of the organisms.

TABLE A–2.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Hugh M. Smith *cruise 43*

Station	Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	*M.*³	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
22–1	Jan. 23	1622–1655	0–145	1991.9	2	5						7
22–2	do	1825–1855	0–145	2023.7	3	1						4
22–3	do	2005–2040	0–158	2104.9		2	2					4
22–4	do	2207–2238	0–140	1711.4	4	11	5					20
22–5	Jan. 24	0013–0048	0–140	2223.4		11	4			1		16
22–6	do	0210–0241	0–141	1887.6	2	13	4				1	20
22–7	do	0408–0438	0–148	1787.0	1	4	2					7
22–8	do	0615–0649	0–158	1716.8		1						1
22–9	do	0803–0832	0–140	1528.0								0
22–10	do	1012–1042	0–149	1568.6		1	1					2
22–11	do	1208–1245	0–158	1986.8								0
22–12	do	1401–1431	0–140	1559.6	2	5					1	8

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

TABLE A–3.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Charles H. Gilbert *cruise 38*

Station	Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	*M.*[3]	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
34–A	Mar. 6	0806–0836	0–140	1885.5	3							3
34–B	do	1003–1033	0–141	1476.7						1		1
34–C	do	1205–1237	0–140	1896.6	3							3
34–D	do	1408–1438	0–140	1938.8	1							1
34–E	do	1608–1636	0–140	1486.8	1							1
34–F	do	1807–1837	0–142	1949.7		1						1
34–G	do	2006–2036	0–142	1902.2	4					1		5
34–H	do	2210–2240	0–140	1624.9	10	1						11
34–I	Mar. 7	0006–0037	0–142	1737.6	5					1		6
34–J	do	0205–0235	0–140	1907.0	8					1		9
34–K	do	0403–0434	0–142	1884.9	14							14
34–L	do	0604–0634	0–140	1703.9	8	3						11
93–A	Apr. 17	1311–1341	0–140	1608.2								0
93–B	do	1503–1533	0–140	1629.9								0
93–C	do	1702–1732	0–140	1512.7								0
93–D	do	1903–1933	0–142	1847.0	4							4
93–E	do	2102–2132	0–140	1630.8								0
93–F	do	2306–2336	0–140	1719.8	2							2
93–G	Apr. 18	0102–0133	0–142	1697.4	2							2
93–H	do	0302–0332	0–142	1668.4	1		1					2
93–I	do	0503–0533	[2]?	1478.7	3							3
93–J	do	0702–0732	0–140	1478.4	3							3
93–K	do	0903–0934	0–142	1696.3	2							2
93–L	do	1102–1132	0–140	1573.3	2							2

[1] SJ—*Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.
[2] Cable meter failed.

TABLE A–4.—*Data on plankton hauls and numbers of larval tunas collected at the diel variability station (9°34′ S., 139°50′ W.) on* Hugh M. Smith *cruise 45*

Station	Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
					SJ	YF	BE	AL	EU	AU	UN	Total
			M.	*M.*[3]	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
120–1	June 8	1522–1552	0–122	937.5	1							1
120–2	do	1522–1552	112–230	606.7								0
121–1	do	1710–1739	0–125	797.5	3							3
121–2	do	1710–1739	96–239	445.0								0
122–1	do	1914–1941	0–126	845.2	3							3
122–2	do	1914–1941	112–238	1041.1								0
123–1	do	2105–2133	0–126	941.4								0
123–2	do	2105–2133	71–238	1003.0								0
124–1	do	2313–2347	0–137	865.6	[2]1							1
124–2	do	2313–2347	103–240	394.6								0
125–1	June 9	0110–0144	0–137	852.6		1						1
125–2	do	0110–[3]?	70–240	1482.7								0
126–1	do	0308–0335	0–121	794.0								0
126–2	do	0308–0335	107–229	598.8								0
127–1	do	0510–0539	0–126	817.8	4							4
127–2	do	0510–0539	103–238	681.1								0
128–1	do	0711–0737	0–125	794.3								0
128–2	do	0711–0737	94–245	447.1								0
129–1	do	0910–0937	0–126	718.5								0
129–2	do	0910–0937	76–238	939.8								0
130–1	do	1108–1149	0–150	855.4								0
130–2	do	1108–1149	71–262	[4]71.3								0
131–1	do	1306–1333	0–123	702.0								0
131–2	do	1306–1333	116–239	920.6								0

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.
[2] A 27-mm. juvenile.
[3] Messenger time was not recorded.
[4] Flowmeter recording was extremely low.

TABLE A–5.—*Data on larval tunas collected during the offshore survey on* Charles H. Gilbert *cruise 35*

Station	Position		Date (1957)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*[3]	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
35	9°16′	137°52′	Oct. 24	2301–2329	0–182	1681.0								0
36	9°16′	137°52′	do	2333–0001	0–140	1546.8								0
38	9°22′	137°30′	Oct. 25	0259–0330	0–140	1316.0								0
38A	9°22′	137°30′	do	0332–0401	0–140	1487.2								0
38B	9°14′	136°20′	do	2256–2327	0–140	1760.4	2	1						3
39	9°14′	136°20′	do	2329–0001	0–140	1797.9	4	1	3					8
41	9°14′	136°34′	Oct. 26	0258–0329	0–173	1750.1	5						3	8
42	9°14′	136°34′	do	0330–0401	0–140	1694.2	2						5	7
44	9°17′	139°02′	do	2259–2329	0–140	1486.1								0
45	9°17′	139°02′	do	2331–0003	0–140	1582.7	[2]1							1
47	9°17′	139°16′	Oct. 27	0254–0324	0–140	1558.2								0
48	9°17′	139°16′	do	0326–0357	0–140	1463.9								0
50	11°03′	139°33′	do	2300–2330	0–140	1530.1	4						1	5
51	11°03′	139°33′	do	2332–0000	0–140	1354.9	2							2
53	11°22′	139°27′	Oct. 28	0258–0328	0–140	1533.9	5							5
54	11°22′	139°27′	do	0330–0401	0–140	1655.9	7						1	8
55	12°23′	139°36′	do	2300–2331	0–140	2011.0								0
56	12°23′	139°36′	do	2332–0000	0–140	1722.6	6							6
58	12°09′	139°30′	Oct. 29	0258–0327	0–140	1527.4	5							5
59	12°09′	139°30′	do	0329–0358	0–140	1453.1	6							6
60	9°36′	139°44′	Oct. 30	0300–0328	0–140	1134.0								0
61	9°36′	139°44′	do	0329–0400	0–140	1336.5	1							1
62A	7°20′	139°32′	Nov. 1	2258–2329	0–140	1663.2	6							6
63	7°20′	139°32′	do	2331–2359	0–140	1414.5	2							2
65	7°06′	139°30′	Nov. 2	0257–0327	0–140	3365.6								0
66	7°06′	139°30′	do	0332–0400	0–140	1633.8								0
67	6°04′	139°50′	do	2257–2327	0–140	1788.8								0
68	6°04′	139°50′	do	2329–0000	0–140	1915.1	2	1					1	4
70	6°26′	139°52′	Nov. 3	0302–0333	0–140	1807.4								0
71	6°26′	139°52′	do	0349–0419	0–140	1755.8	6							6
73	8°36′	139°31′	do	2305–2334	0–140	1390.0	8							8
74	8°36′	139°31′	do	2335–0005	0–140	1408.0	5					2		7
76	8°54′	139°38′	Nov. 4	0300–0330	0–140	854.4	2					3		5
77	8°54′	139°38′	do	0334–0404	0–140	715.8								0
79	9°13′	141°35′	do	2258–2328	0–140	2218.6	14			1			2	17
80	9°13′	141°35′	do	2331–0002	0–140	2168.1	14	1						15
82	9°12′	142°00′	Nov. 5	0256–0326	0–140	1813.9	1							1
83	9°12′	142°00′	do	0328–0356	0–140	1786.6	1							1
84	9°15′	142°46′	do	2259–2329	0–140	1490.9								0
85	9°15′	142°46′	do	2332–0004	0–140	1580.6								0
87	9°18′	142°23′	Nov. 6	0258–0329	0–140	1496.6	3						1	4
88	9°18′	142°23′	do	0334–0403	0–140	1449.6	12							12
90	9°15′	140°33′	do	2256–2326	0–140	1267.4	1							1
91	9°15′	140°33′	do	2328–2358	0–140	1192.9								0
93	9°13′	140°10′	Nov. 7	0258–0328	0–140	1264.4	4						1	5
94	9°13′	140°10′	do	0332–0402	0–140	1074.6	6							6

[1] SJ—*Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.
[2] A juvenile about 25 mm. long.

TABLE A–6.—*Data on larval tunas collected during the offshore survey on* Hugh M. Smith *cruise 43*

Station	Position		Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*[3]	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
30	9°12′	139°17′	Jan. 27	2116–2151	0–141	1755.7								0
32	9°12′	138°48′	Jan. 28	0313–0342	0–160	1300.0	2		2				1	5
34	9°10′	136°50′	do	2110–2140	0–147	1750.6	13	1						14
36	9°10′	136°18′	Jan. 29	0313–0343	0–145	1617.9	6							6
39	9°37′	139°40′	Jan. 30	2109–2139	0–148	1688.4								0
41	10°14′	139°38′	Jan. 31	0312–0342	0–148	1516.8	3							3
42	12°02′	139°36′	do	2112–2142	0–154	1466.3	10							10
44	12°31′	139°34′	Feb. 1	0313–0343	0–185	1158.6	3							3
47	11°16′	139°42′	do	2110–2141	0–141	1551.1	12	3					2	17
49	10°43′	139°39′	Feb. 2	0313–0343	0–141	582.7	3		1					4
57	9°07′	141°05′	Feb. 5	2118–2145	0–141	1264.6								0
59	9°08′	141°32′	Feb. 6	0319–0344	0–142	1384.6								0
60	9°13′	143°02′	do	2113–2143	0–140	1403.1	13							13
62	9°15′	142°26′	Feb. 7	0315–1337	0–145	1468.9	6							6
64	9°13′	140°41′	do	2109–2133	0–167	1039.8	2							2
66	9°16′	140°06′	Feb. 8	0318–0348	0–140	1511.9								0
70	7°35′	139°40′	Feb. 9	2110–2137	0–140	1164.9	13	1						14
71	6°52′	139°40′	Feb. 10	0330–0359	0–141	1386.1	3							3
73	5°37′	139°50′	do	2113–2142	0–140	1363.7	8	1						9
75	6°21′	139°38′	Feb. 11	0319–0347	0–141	1279.6	1							1
76	8°30′	139°40′	do	2120–2146	0–140	957.7	1							1
78	9°03′	139°45′	Feb. 12	0312–0341	0–140	1199.9	5	1				4		10

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

TABLE A–7.—*Data on larval tunas collected during the offshore survey on* Charles H. Gilbert *cruise 38*

Station	Position		Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*[3]	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
46	9°11′	138°06′	Mar. 26	2204–2234	0–140	1416.2								0
48	9°09′	137°34′	Mar. 27	0405–0435	0–142	1647.2	1							1
49	9°11′	136°15′	do	2104–2135	0–142	1703.6	5							5
51	9°07′	136°56′	Mar. 28	0304–0334	0–140	1776.7	6							6
53	9°09′	138°53′	do	2122–2151	0–140	1394.2								0
55	9°08′	139°27′	Mar. 29	0303–0332	0–140	1338.6	14	2						16
57	7°32′	139°46′	do	2104–2134	0–142	1275.6	29		10					39
59	6°57′	139°44′	Mar. 30	0305–0336	0–142	1363.8	2							2
60	5°44′	139°40′	do	2102–2132	0–140	1644.4	4							4
62	6°20′	139°39′	Mar. 31	0307–0337	0–140	1505.8	12		5	1				18
64	8°10′	139°44′	do	2103–2133	0–142	1475.9	13	2	1					16
66	8°38′	139°57′	Apr. 1	0306–0336	0–142	1456.4	8							8
69	9°08′	141°14′	Apr. 3	2104–2134	0–140	1543.7	1							1
71	9°07′	141°52′	Apr. 4	0309–0339	0–140	1751.3	6							6
72	9°05′	142°58′	do	2102–2133	0–142	1885.5	9							9
74	9°04′	142°28′	Apr. 5	0304–0334	0–142	1657.8	3							3
75	9°09′	140°28′	do	2103–2132	0–140	1212.8								0
77	9°12′	139°57′	Apr. 6	0309–0339	0–140	1333.3	8							8
78	10°52′	139°45′	do	2107–2137	0–142	1407.8								0
80	11°28′	139°48′	Apr. 7	0304–0335	0–140	1627.7	6							6
81	12°32′	139°43′	do	2103–2133	0–140	1546.5	5	1						6
83	12°00′	139°41′	Apr. 8	0305–0335	0–140	1921.8	12							12
84	10°02′	139°44′	do	2100–2130	0–142	1406.7	1							1
86	9°24′	139°51′	Apr. 9	0302–0332	0–142	1536.7	6							6

[1] SJ = *Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

TABLE A–8.—*Data on larval tunas collected during the offshore survey on* Hugh M. Smith *cruise 45*

Station	Position		Date (1958)	Collection time (+9ZT)	Depth of tow	Water strained	Larvae in sample[1]							
	Lat. S.	Long. W.					SJ	YF	BE	AL	EU	AU	UN	Total
					M.	*M.*[3]	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
78	9°08′	138°10′	May 15	2004–2030	0–140	1392.8	4							4
79	9°12′	137°22′	May 16	0317–0346	0–161	1611.1	34							34
82	9°10′	136°10′	do	2000–2028	0–140	1432.8	6	2						8
83	9°13′	137°02′	May 17	0320–0347	0–139	1321.9	2							2
84	9°12′	139°07′	do	1959–2029	0–125	1601.3	3		1					4
87	9°12′	141°22′	May 19	2000–2029	0–140	1578.1								0
88	9°12′	142°02′	May 20	0313–0343	0–137	1357.3								0
90	9°12′	143°08′	do	1955–2026	0–140	1536.0			2	1				3
91	9°14′	142°20′	May 21	0309–0338	0–140	1592.1	4		3	5				12
94	9°12′	140°36′	do	2002–2031	0–137	1359.1	1							1
97	7°39′	139°45′	May 23	2001–2030	0–140	1421.6	1		9					10
98	6°54′	139°41′	May 24	0314–0343	0–140	1426.5								0
101	5°38′	139°40′	do	1958–2028	0–138	1491.0	2		3				1	6
102	6°24′	139°38′	May 25	0310–0344	0–140	1759.2	2	1						3
105	8°25′	139°42′	do	1959–2034	0–137	1926.3	2							2
107	10°55′	139°40′	May 27	2000–2028	0–139	1301.2	4							4
108	11°30′	139°39′	May 28	0312–0339	0–144	2165.0								0
110	12°41′	139°39′	do	2001–2040	0–133	2347.5								0
111	11°58′	139°40′	May 29	0306–0336	0–124	1459.1								0
113	10°11′	139°34′	do	1953–2025	0–140	1928.4	15		1					16
114	9°25′	139°34′	May 30	0315–0351	0–146	944.9							1	1

[1] SJ—*Katsuwonus pelamis;* YF = *Thunnus albacares;* BE = *Thunnus obesus;* AL = *Thunnus alalunga;* EU = *Euthynnus affinis;* AU = *Auxis* sp.; UN = unidentified tuna.

ASSOCIATION OF FISHES WITH FLOTSAM IN THE OFFSHORE WATERS OF CENTRAL AMERICA

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ABSTRACT

During April, May, June, and October, 1963, a total of 70 purse seine collections were made of the fishes associated with floating objects. Nearly all of these collections were from the offshore waters of Costa Rica. Twelve families of fishes (Lobotidae, Carangidae, Coryphaenidae, Mullidae, Kyphosidae, Pomacentridae, Scombridae, Blenniidae, Stromateidae, Mugilidae, Polynemidae, and Balistidae) and 32 species were represented in the collections. Most of the species were present during both spring and fall, and nearly all of the fishes were juveniles.

Nine of the 32 species, including the 2 most abundant ones, *Caranx caballus* Günther and *Selar crumenophthalmus* (Bloch), were carangids. The lengths of two species, *Abudefduf saxatilis* (Linnaeus) and *Seriola* sp. were greater the farther an object was located from shore. Some species such as *C. caballus, Psenes pacificus* Meek and Hildebrand, and *Canthidermis maculatus* (Bloch) were present in almost a complete series of juvenile stages; others as *Chromis atrilobata* Gill, *Pseudupeneus grandisquamis* (Gill), and *Agonostomus monticola* (Bancroft) were represented by only a single juvenile stage. More fishes were collected under large objects than under small objects. The total number of individuals present near moored objects after 5 days did not differ from the numbers present after 20 or more days. The coloration of fishes was related to their association behavior. Silvery colored fishes did not remain as close to the object as did the more darkly colored species. Most adult fishes, which did not remain as near the object as did juveniles, appeared beneath an object only intermittently. *Canthidermis maculatus,* however, maintained close contact with drifting objects both as adults and juveniles.

Observations of the behavior of species are discussed in relation to the mechanisms for the association of fish with flotsam that have been postulated by other authors. None of their hypotheses was supported by our data. Additional mechanisms were postulated.

The association of fishes with floating objects has been exploited by a number of fisheries. Japanese pole-and-line fisheries and American purse seine and live-bait fisheries take advantage of the association of yellowfin tuna, *Thunnus albacares* (Bonnaterre), and oceanic skipjack, *Katsuwonus pelamis* (Linnaeus), with algae, logs, and other flotsam (Uda, 1933; McNeely, 1961). Uda and Tsukushi (1934), and Yabe and Mori (1950) reported that log-associated schools of tuna provide a consistently higher yield per unit fishing effort than unassociated schools.

Moored rafts of bamboo or palm fronds are used to attract dolphin-fish, *Coryphaena hippurus* (Linnaeus), in seine fisheries of Japan (Kojima, 1955, 1956, 1960a, 1960b, and 1961). Moored cork-slabs serve the same purpose for Maltese fishermen (Galea, 1961). Two types of palm-frond rafts are used by Indonesian fishermen to attract various clupeids, scombrids, *Decapterus* spp., and other carangids (Hardenberg, 1950; Soemarto, 1960). In addition to these commercially important species, many others of lesser or no commercial value are also encountered (Murray and Hjort (1912), Yabe and Mori (1950), Uchida and Shojima (1958), Besednov (1960), Kojima (1960a), Mansueti (1963), and Gooding and Magnuson[1]).

Note: Approved for publication March 8, 1966.

[1] Reginald M. Gooding and John J. Magnuson—Observations on the ecology and behavior of fishes around a drifting raft near Hawaii during the first 48 hours adrift. Manuscript, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

Gooding and Magnuson reviewed the hypotheses that have been advanced to explain this habit: (1) attraction by food (smaller fish, algae, decaying palm fronds, and plankton made more visible by the shade of the object); (2) negative phototaxis in response to the shadow cast by the object; (3) shelter from predators; and (4) use of the object as a spawning substrate. They also suggested an additional hypothesis that floating objects are cleaning stations where pelagic fishes go to have their parasites removed by other fish.

This paper provides information on the ecology and behavior of fishes associated with floating objects in the offshore waters of Central America. Special attention is given to the frequency, abundance, and size of the species which compose flotsam-associated aggregations and how these characteristics are related to the location and size of the object. These studies are the framework upon which future behavior investigations will be based. The aim of our program is to determine whether a device can be designed that will be maximally efficient in aggregating tuna and skipjack. The potential value to the tuna fishery of establishing such devices has been discussed by Alverson and Wilimovsky (1963).

PROCEDURES

Nearly all of our studies were in the offshore waters of Costa Rica (fig. 1) because yellowfin tuna and skipjack are often associated with the flotsam in this region (logbook records obtained through the courtesy of the Inter-American Tropical Tuna Commission). Several collections were near the coast of southern Mexico and 1 near Cocos Island. Samples were collected by encircling flotsam and its associated fauna with a small 7/16-inch (11 mm.) stretch-mesh purse seine, 12 feet deep (3.7 m.) and 110 feet (33.5 m.) long (Aasted, MS.)[2]. An average of 66 percent of the fishes observed beneath an object were captured in the seine. Fish larger than 100 mm. standard length may have escaped the net, and fish smaller than 15 mm. occasionally swam through the webbing. When the net was set, fish tended to stay near the flotsam or even swim upward. Thus, fish swimming at a depth greater than the maximum depth of the seine also may have been caught. Sampling errors due to fish escaping from or entering the seined cylinder of water were probably small.

[2] Donald C. Aasted, A miniature purse seine for capturing small pelagic fishes. Manuscript, Bureau of Commercial Fisheries Tuna Resources Laboratory, La Jolla, Calif.

Twenty-three purse seine collections of fishes were made during April, May, and June, 1963, and 47 during October. Of these samples, 62 were of fishes associated with naturally occurring flotsam, and 8 were of fishes collected beneath moored logs, buoys, and other objects.

After a collection was made, the success of the set was estimated, the object was described and measured, and motile and attached organisms were preserved. In the October studies, to determine the rate and direction of movement of drifting materials, all objects were tagged and marked with a small flag prior to release. Underwater observations and cinematic photographs were used to describe the behavior and estimate the abundance of fishes.

CHARACTERISTICS AND DISTRIBUTION OF FLOTSAM

Far more drifting materials were in the study area in October than in the spring. The Gulf of Nicoya was littered with floating logs and other plant debris. The greater abundance of flotsam in October was not surprising because rainfalls are usually heaviest during this period (Peterson, 1960).

Fish were not seen beneath the flotsam in the Gulf and were only rarely associated with inshore logs between Cape Blanco and Piedra Blanca (fig. 1). Northwest of this area, however, nearly every drifting object encountered had its own associated fish population. Most often these objects were aggregated in areas of current convergence.

During April, May, and June, currents in the area usually set northwest at an estimated 2 knots; currents also set northwest during October but were not as strong. Three logs tagged in October and later recovered had drifted northwest at 0.28, 0.45, and 0.33 knot.

Only one of the drifting objects sampled had attached invertebrates—goose barnacles, *Conchoderma virgatum* (Spengler). This species and other goose barnacles of the genus *Lepas* were found in quantity on moored objects after 14 or more days.

Adult and megalops grapsoid crabs of the genus *Plagusia* were numerous on nearly all logs. Individuals in the megalops stage frequently were swimming near drifting objects.

SEASONAL VARIATION IN OCCURRENCE OF FISH

Over 12,000 fishes were captured beneath floating objects in this study; 12 families and 32 species were

FIGURE 1.—Positions of collections made of fishes beneath flotsam in April, May, and June 1963 (spring) and October 1963 (fall). Numerals indicate number of collections made in each locality. Inset at top shows location of study area and position of the six collections made outside this area.

represented. The scientific name, family, and season of occurrence of these species are presented in table 1. Abbreviated names are used in the text and subsequent tables.

There was little seasonal variation in the occurrence of species. Twenty-four of the total of 32 species were captured or observed during both spring and fall. The seasonal occurrence of adult

TABLE 1.—*Length, life stage, and seasonal occurrence of species collected beneath flotsam in the offshore waters of Central America*[1] *in 1963*

Species	Life stage		Total captured	Range of standard length	Season	
	Adult	Juvenile			Spring	Fall
			Number	*Mm.*		
Lobotidae (tripletails)						
Lobotes pacificus Gilbert	–	x	3	72–246	–	x
Carangidae (jacks and scads)						
Caranx caballus Günther	x[2]	x	6,215	9–212	x	x
Caranx hippos (Linnaeus)	–	x	105	16–85	x	x
Caranx marginatus (Gill)	–	x	44	17–101	x	x
Decapterus sp.[3]	–	x	298	17–100	x	x
Elagatis bipinnulatus (Quoy and Gaimard)	–	x	218	11–263	x	x
Naucrates ductor (Linnaeus)	–	x	43	29–143	x	x
Selar crumenophthalmus (Bloch)	x[2]	x	1,348	15–108	x	x
Seriola colburni (Evermann and Clark)	–	x	5	103–154	x	–
Seriola sp.[3]	–	x	315	10–163	x	x
Coryphaenidae (dolphins)						
Coryphaena equiselis Linnaeus	–	x	5	35–68	x	–
Coryphaena hippurus Linnaeus	x[2]	x	2	34–42	x	x
Mullidae (goatfishes)						
Pseudupeneus grandisquamis (Gill)	–	x	339	26–54	x	x
Kyphosidae (sea chubs)						
Kyphosus analogus (Gill)	–	x	3	63–137	x	x
Kyphosus elegans (Peters)	–	x	22	32–103	x	x
Kyphosus sp.[3]	–	x	2	18–59	x	x
Sectator ocyurus (Jordan and Gilbert)	x[4]	x	248	17–253	x	x
Pomacentridae (damselfishes)						
Abudefduf saxatilis (Linnaeus)	–	x	437	8–46	x	x
Chromis atrilobata Gill	–	x	1,449	21–32	x	x
Scombridae (mackerels and tunas)						
Auxis thazard (Lacépède)	–	x	1	48	x	–
Euthynnus lineatus Kishinouye	x[4]	x	7	37–477[5]	x	x
Katsuwonus pelamis (Linnaeus)	x[4]	–	435	230–597[5]	–	x
Thunnus albacares (Bonnaterre)	x[4]	–	149	500–750[5]	x	–
Blenniidae (combtooth blennies)						
Blenniolus brevipinnis (Günther)	x	x	39	13–31	x	x
Stromateidae (butterfishes)						
Psenes pacificus Meek and Hildebrand	–	x	822	10–133	x	x
Mugilidae (mullets)						
Agonostomus monticola (Bancroft)	–	x	38	11–30	–	x
Mugil curema Valenciennes	–	x	6	18–47	x	x
Polynemidae (threadfins)						
Polydactylus approximans (Lay and Bennett)	–	x	30	23–47	x	x
Polydactylus opercularis (Gill)	–	x	1	40	–	x
Monacanthidae (filefishes)						
Alutera monoceros (Linnaeus)	x[2]	x	1	107	–	x
Alutera scripta (Osbeck)	x[2]	x	1	72	–	x
Balistidae (triggerfishes)						
Balistes polylepis Steindachner	–	x	9	28–184	x	x
Canthidermis maculatus (Bloch)	x	x	178	30–236	x	x

[1] Specimens cataloged in Marine Vertebrates collection, Scripps Institution of Oceanography.
[2] Adults observed but not captured.
[3] Specific name unknown.
[4] Adults collected by method other than small purse seine.
[5] Fork length.

scombrids can be ascribed to variation in collection methods rather than to seasonal differences. Adult frigate mackerel, *Auxis thazard*, black skipjack, *Euthynnus lineatus*, oceanic skipjack, and yellowfin tuna were present during both seasons, and all are known to associate with flotsam.

The mountain mullet, *Agonostomus monticola*, was not in the spring collections but occurred in 10 of the 47 fall collections. This species inhabits marine waters only as a prejuvenile (Ebeling, 1961). Thus its occurrence in only the fall collections could be due to a seasonal difference in reproductive activities.

The remainder of the species that were taken during only 1 season were relatively uncommon in the collections. Their absence during 1 season could be due to chance alone.

LIFE STAGE OF FISHES ASSOCIATED WITH FLOTSAM

Nearly all of the fishes observed and captured beneath drifting objects were juveniles; however, adult sharks, *Carcharhinus limbatus* (Müller and Henle) and *Carcharhinus azureus* (Gilbert and Starks), and schools of adult *Caranx caballus*, *Selar crumenophthalmus*, *Coryphaena hippurus*, *Sectator ocyurus*, and *Euthynnus lineatus* were observed. With the exception of *S. ocyurus*, these adults did not swim as close to the object as did the smaller fishes, and they remained near it only for short periods. None of these adults were captured by the small purse seine. Some were captured, however, by other methods. Owing to the infrequent capture of these adults and to the difficulty of ascertaining whether or not they were in fact associated with a particular object, our presentation is limited to the fishes captured by the small seine. *Canthidermis maculatus* was the only species that frequently occurred both as adult and juvenile; both stages were captured in the seine.

To determine if the size of the fishes was related to the distance of an object from shore, the shortest distance to the shore from the location of each collection was measured to the nearest nautical mile. The length measurements of species from different collections captured at the same distance from shore were combined, and a mean and range were established (figs. 2, 3, and 4).

The mean and minimum length of *Abudefduf saxatilis* and *Seriola* sp. increased with the distance of an object from shore (chi-square test for two independent samples, $p<.01$)—figs. 2 and 3. The

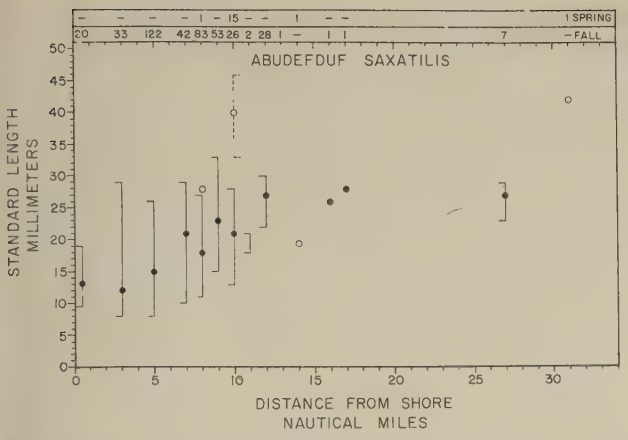

FIGURE 2.—Range and mean standard length of *Abudefduf saxatilis* collected beneath flotsam in the offshore waters of Central America at various distances from shore. Broken lines indicate range for spring collection, solid lines, range for fall collections. Open circles indicate mean for spring, filled circles, mean for fall; circles without bars indicate single fish. Upper numerals are total number of *Abudefduf* captured in spring of 1963, lower numerals, fall 1963.

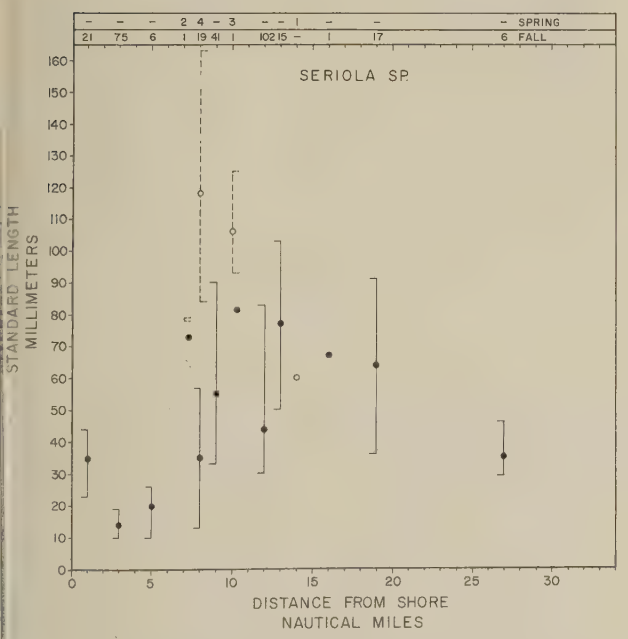

FIGURE 3.—Range and mean standard length of *Seriola* sp. collected beneath flotsam in the offshore waters of Central America at various distances from shore. Broken lines indicate range for spring collections, solid lines range for fall collections. Open circles indicate mean for spring, filled circles, mean for fall; circles without bars indicate single fish. Upper numerals are total number of *Seriola* sp. captured in spring of 1963, lower numerals, fall of 1963.

maximum size of these two species did not show this change. The mean length of *Selar crumenophthalmus* also increased with distance, but this change was not as marked as in the other two species (fig. 4).

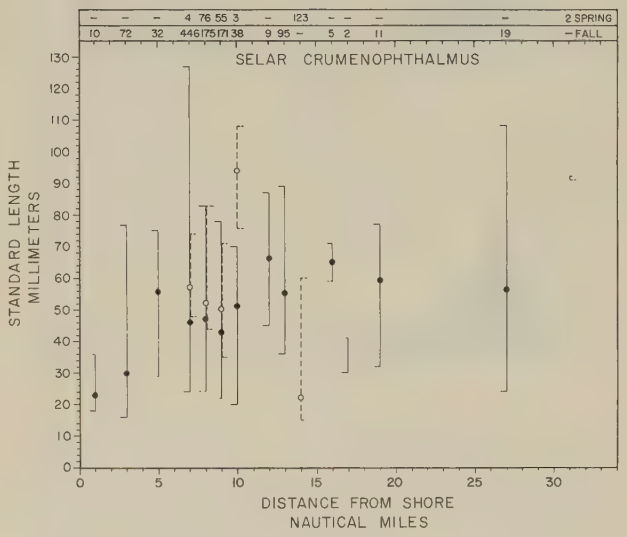

FIGURE 4.—Range and mean standard length of *Selar crumenophthalmus* collected beneath flotsam in the offshore waters of Central America at various distances from shore. Broken lines indicate range for spring collections, solid lines, range for fall collections. Open circles indicate mean for spring, filled circles, mean for fall. Upper numerals are total number of *Selar* captured in spring of 1963, lower numerals, fall of 1963.

Abudefduf saxatilis spawns inshore on rocks or reefs, and the males defend the clutch of eggs (R. Rosenblatt, personal communication); thus, larvae and juveniles of this species may be more abundant inshore. It seems possible that individuals captured offshore were originally recruited to the object inshore and accompanied it as it drifted away from land. The larger size of the offshore specimens could be attributed to growth while the fish were associated with the object.

In the remainder of the fishes no obvious relation was evident between the distance from shore and the minimum or mean length; however, the ranges of sizes at which these fishes were associated with flotsam differed widely. Some species were represented by almost a complete series of juvenile stages. *Caranx caballus* and *Psenes pacificus* are good examples of this group (fig. 5). Less abundant species in this group were *Elagatis bipinnulatus*, *Kyphosus elegans*, *Sectator ocyurus*, and *Canthidermis maculatus*

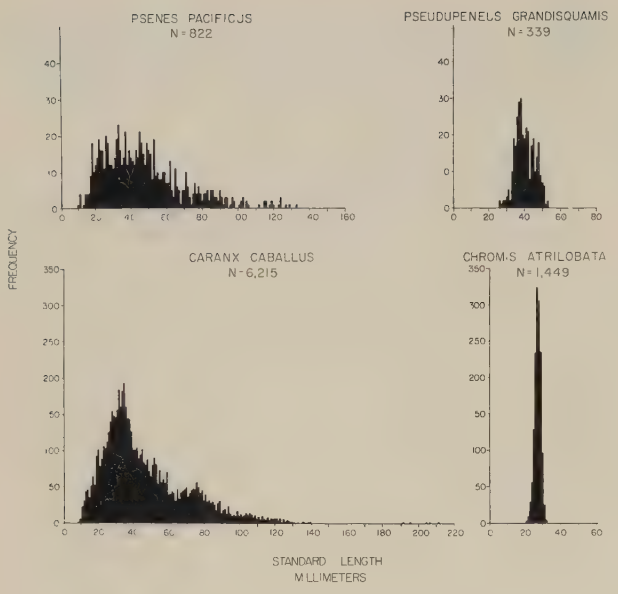

FIGURE 5.—Length frequency for *Psenes pacificus*, *Pseudupeneus grandisquamis*, *Caranx caballus*, and *Chromis atrilobata*. Numbers are totals for combined spring and fall collections.

(table 1). The size range of juveniles of other species was extremely restricted. *Chromis atrilobata* and *Pseudupeneus grandisquamis* had this compact type of size distribution (fig. 5). Other species, not figured, which also had a limited size range included *Agonostomus monticola*, *Polydactylus approximans*, and *Blenniolus brevipinnis*. *Pseudupeneus*, *Chromis*, *Agonostomus*, and *Polydactylus* have pelagic juvenile stages but as adults inhabit other areas. The upper size limit of these species in our collections probably was determined by the size at which they end the pelagic phase of their lives.

Blenniolus brevipinnis is a small species; females 19.5 mm. long can be sexually mature (Krejsa, 1960). Adults and juveniles have been found near drifting logs as well as among rocks and coral heads in inshore areas (Krejsa, 1960). Apparently for both adults and juveniles of this species, drifting objects are a suitable pelagic substitute for inshore habitats.

FREQUENCY, ABUNDANCE, AND DOMINANCE OF FISHES COLLECTED BENEATH FLOTSAM

The characters used by Fager and McGowan (1963) for the analysis of zooplankton populations were used to describe the structure of the flotsam-associated aggregations of fish: (1) frequency—the total number of collections in which a species occurred; (2) abundance—the range and median of the numbers of individuals per collection in which the species was found; and (3) dominance—the number of samples in which a particular species or a group including this species comprised 50 percent or more of the total number of individuals in a given collection. As the structure of the populations in the spring was similar to that in the fall, the two series of collections were combined to calculate these statistics.

Fifteen of the 32 species had frequencies greater than 10. These were ranked from 1 to 15 on the basis of their frequency, median abundance, and dominance. Tied values were given the average of the ranks (table 2 and fig. 6). The remainder of the species was ranked only by frequency (table 3).

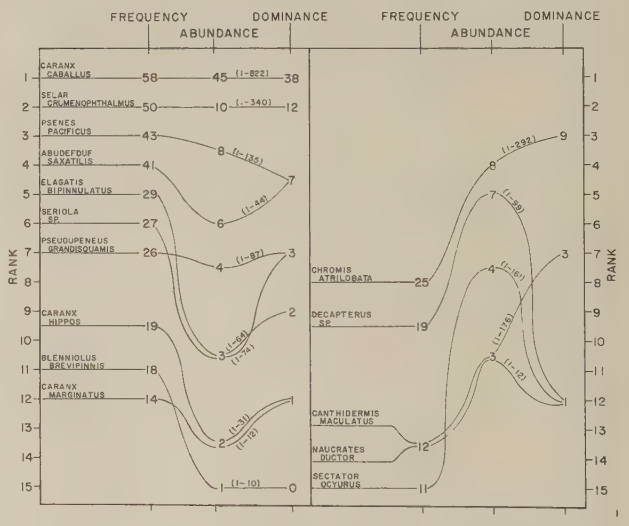

FIGURE 6.—Ecological characters of the 15 species most frequently captured beneath flotsam in the offshore waters of Central America in 1963. Each species was ranked separately by: *frequency*, the total number of collections in which the species occurred; *abundance*, median of the numbers of individuals per collection in which the species was found; and *dominance*, the number of collections in which a species was among those making up 50 percent of the individuals. Lines indicate the rank held by each species in the three rankings. Values upon which ranks were based are shown in each column. In the second column, parentheses enclose the range of the number of individuals per collection of occurrence. For clarity, we separated the 15 species into 2 groups: left half of figure, species whose ranked abundance was the same as or lower than the ranked frequency; and right half, species whose ranked abundance was higher than the ranked frequency. The total number of collections was 70.

TABLE 2.—*Ecological characters of the 15 most frequently captured species collected beneath flotsam in the offshore waters of Central America in 1963*[1]

Species	Frequency[2]	Rank[3]	Abundance		Rank[3]	Dominance[4]	Rank[3]
			Range[5]	Median[6]			
Caranx caballus	58	1	(1–822)	45	1	38	1
Caranx hippos	19	9.5	(1–31)	2	13.5	1	12
Caranx marginatus	14	12	(1–12)	2	13.5	1	12
Decapterus sp.	19	9.5	(1–99)	7	5	1	12
Elagatis bipinnulatis	29	5	(1–64)	3	10.5	2	9
Naucrates ductor	12	13.5	(1–12)	3	10.5	1	12
Selar crumenophthalmus	50	2	(1–340)	10	2	12	2
Seriola sp.	27	6	(1–74)	3	10.5	3	7
Pseudupeneus grandisquamis	26	7	(1–87)	4	7.5	3	7
Sectator ocyurus	11	15	(1–161)	4	7.5	1	12
Abudefduf saxatilis	41	4	(1–44)	6	6	7	4.5
Chromis atrilobata	25	8	(1–292)	8	4	9	3
Blenniolus brevipinnis	18	11	(1–10)	1	15	0	15
Psenes pacificus	43	3	(1–135)	8	3.5	7	4.5
Canthidermis maculatus	12	13.5	(1–176)	3	10.5	3	7

[1] The total number of collections was 70.
[2] The total number of collections in which the species occurred.
[3] Rank based on figures in adjacent columns.
[4] The number of samples in which a particular species or a group including this species comprised 50 percent or more of the total number of individuals in a given collection.
[5] Range of the numbers of individuals per collection in which species was found.
[6] Median of the numbers of individuals per collection in which species was found.

TABLE 3.—*Frequency, abundance, and dominance of species occurring in 10 or fewer collections made in the offshore waters of Central America in 1963. Listed in order of frequency*

Species	Frequency	Abundance[1]	Dominance
Agonostomus monticola	10	1 (1–11)	0
Polydactylus approximans	9	1 (1–12)	0
Kyphosus elegans	8	1 (1–12)	0
Mugil curema	5	1 (1–2)	0
Balistes polylepis	5	1 (1–4)	0
Kyphosus analogus	3	1 (1)	0
Lobotes pacificus	3	1 (1)	0
Seriola colburni	2	– (2–3)	0
Coryphaena hippurus	2	– (1)	0
Coryphaena equiselis	2	– (2–3)	2
Kyphosus sp.	2	– (1)	0
Polydactylus opercularis	1	– (1)	0
Auxis thazard	1	– (1)	0
Euthynnus lineatus	1	– (1)	0
Alutera monoceros	1	– (1)	0
Alutera scripta	1	– (1)	0

[1] Figures in parentheses show range in number of individuals per collection of occurrence.

Nine of the 32 species were carangids, and all but 1 of these, *Seriola colburni*, were among the 15 most frequent species. The carangid, *C. caballus* was by far the most frequent, abundant, and dominant species collected. This fish contributed 50 percent or more of the individuals in more than half of the collections. *Selar crumenophthalmus*, also a carangid, ranked second in frequency, abundance, and dominance. No other family was represented as frequently in the collections. The family Kyphosidae was represented by four species but only one, *Sectator ocyurus*, occurred in more than 10 collections.

On the basis of their rank by frequency, abundance, and dominance, the 15 most frequent species can be divided into three groups: (1) species that occupied about the same rank in all three categories; (2) species that were captured frequently but were not abundant in the collections in which they occurred; and (3) species captured less frequently that were abundant in the collections in which they occurred. The three highest ranking species, *C. caballus*, *Selar crumenophthalmus*, and *Psenes pacificus* were in the first group. *Abudefduf saxatilis* and *Blenniolus brevipinnis* exemplify the second group, and *Chromis atrilobata* and *Canthidermis maculatus* the third.

The factors responsible for the differences in frequency and abundance of species are unknown. For some species, evidence suggested that schooling was a significant factor. All of the 15 most frequently captured species, except *Abudefduf* and *Blenniolus*, schooled either with their own or other species beneath flotsam. *Abudefduf* remained near the object and appeared to defend small territories; *Blenniolus* maintained contact with the surface of the object and were not aggregated. Possibly the solitary or individual habits of these species were responsible for their lower abundance. Juvenile *Chromis* school at the stage at which they associate with flotsam. This species was dominant in seven of eight collections made in the same area on the same day. The median number of individuals in these seven collections was 199. *Chromis* was dominant only once in the remainder of the collections, and the median number of fish per collection was two. The irregular abundance of *Chromis* could be ascribed to a tendency toward the recruitment of an entire school.

Canthidermis maculatus also was a schooling species and tended to be abundant in the collections in which it occurred. This species did not show the limited temporal and regional abundance described for juvenile *Chromis*, but the distribution of *Canthidermis* appeared to extend farther to sea than other species. The collection farthest from shore (200 nautical miles) contained 87 *Canthidermis* and 4 *Balistes polylepis*. Only *Canthidermis* was observed beneath other drifting material in the same area. The four *B. polylepis* were located inside the cavity of a large bamboo stem and probably did not represent a usual component of high-seas aggregations. Had we taken more collections from flotsam drifting 100 or more nautical miles from shore we feel the frequencies for *Canthidermis* would have increased proportionately.

Decapterus sp. ranked fifth in abundance but only once dominated a collection. This species nearly always schooled with *Selar crumenophthalmus* but was less abundant in the mixed schools. *Decapterus* was captured without *Selar* in only 7 of 19 collections. Thus whenever a large number of *Decapterus* was taken, the number of *Selar* was usually larger. Hence, *Decapterus* rarely dominated a collection.

The use of only the numbers of individuals for the determination of dominance instead of numbers and weights obscured some of the relations among species. Had weights as well as numbers been used, *Canthidermis* and *Psenes* probably would have dominated more collections and *Chromis*, *Pseudupeneus*, and *Abudefduf* fewer. Owing to their large size range and abundance, little difference would be expected in the values for *C. caballus* and *Selar*.

OBJECT SIZE

To determine if the length or the number of fishes was related to the size of the object, we recorded for each collection the volume of the object in cubic centimeters, the total number of fishes captured, and the mean length of all fishes in the collection. Of the two variables only the number of individuals in the collection was obviously related to the volume of the object. Collections made beneath large objects tended to be larger than those taken beneath smaller objects (table 4).

Field observations indicated that the frequency of occurrence of larger fishes may be related to the size of the object. The largest object studied, an entire tree, was too large to be encompassed by the purse seine. The tree was 1 m. in diameter at the root section, had a trunk diameter of 0.3 m. and was over 10 m. long. Associated with the tree was the largest aggregation of adult fishes seen during the study. There were large schools of adult *Sectator ocyurus*, *Canthidermis maculatus*, *Coryphaena hippurus*, and *Euthynnus lineatus* in addition to numerous juvenile fishes. A portion of the school of adult *Sectator* is shown in figure 7A, and in 7B some of the adult *Canthidermis* are shown among the branches of the tree. For comparison, two groups of juvenile fishes that were associated with two smaller objects are pictured in 7C and 7D. Yabe and Mori (1950) captured, by hook and line, fishes associated with a tree of similar dimensions (1 m. in diameter at the butt and 15 m. long). The lengths of the fish of the species they captured exceeded the lengths of the fish in our purse seine collections by about a factor of 10. In our study, the juvenile fishes that were associated with the tree were of the same species and about the same size as those collected beneath smaller objects. Thus the size of the object appeared to be related to the presence or absence of large or adult fishes rather than differences among juveniles.

TABLE 4.—*Number of collections made of fishes associated with objects of three size classes and the number of fishes these collections contained*

[Collections were made in the offshore waters of Central America in 1963]

Fish in collection	Collections from objects of different volume (cubic centimeters)			Total
	101–5,000	5,001–100,000	100,001–5,000,000	
Number	Number	Number	Number	Number
1–10	5	3	0	8
11–100	2	14	6	22
101–1000	0	19	19	38
Total	7	36	25	68[1]

[1] Two collections omitted owing to lack of volume measurements.

ARTIFICIAL MOORED OBJECTS

To study the rate of recruitment of fishes to floating materials, eight objects of various types were moored near the Costa Rican coast for periods of 15 hours to 46 days. Six objects were not visited from the time they were moored until the day the collection was made. Two balsa logs were moored in the same locality at the same time and were observed daily until collections were made on the fifth day.

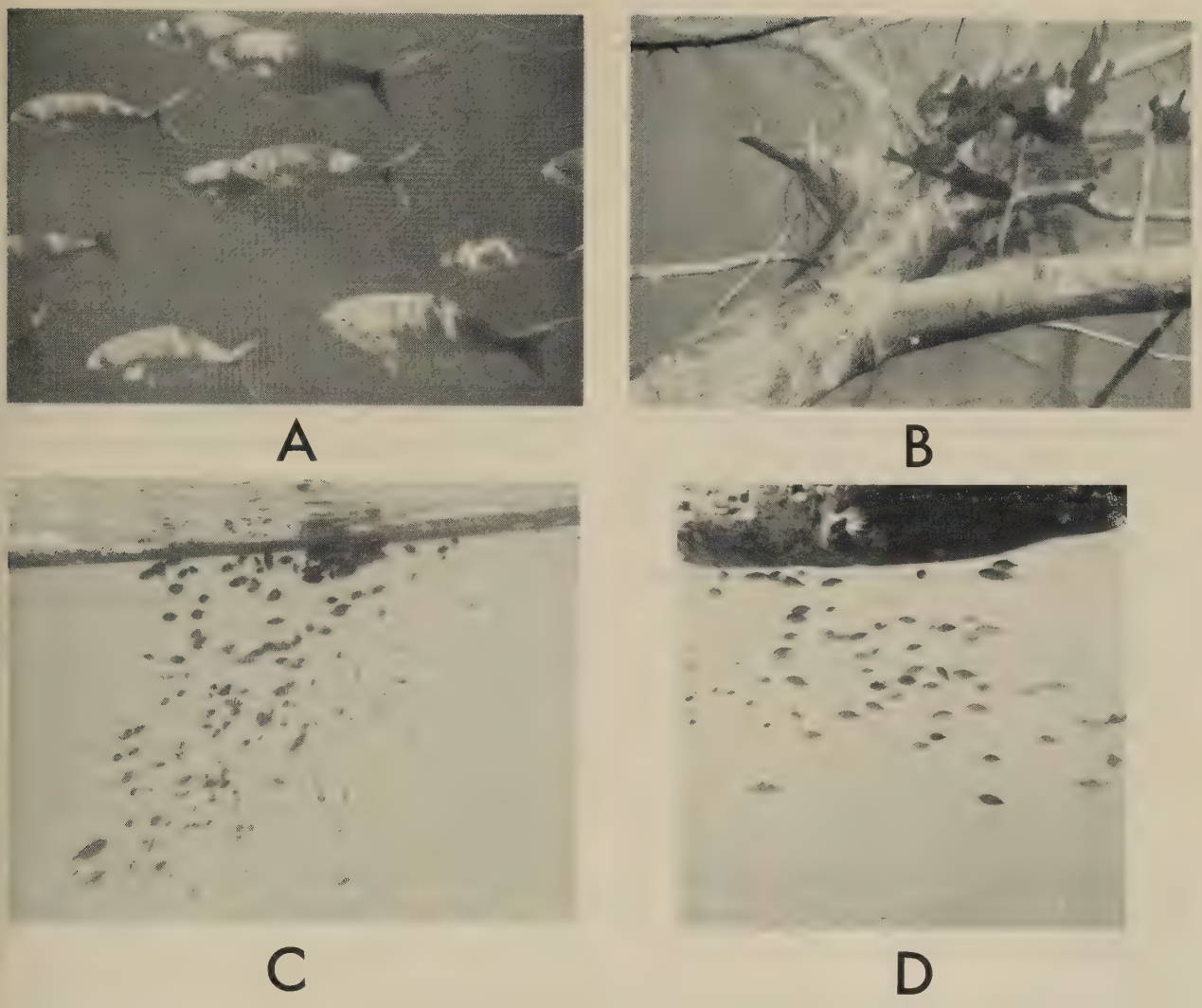

FIGURE 7.—Fishes associated with drifting objects in the offshore waters of Central America in 1963. A, a school of adult *Sectator ocyurus* associated with an entire tree; the small fish in background were juvenile *Selar crumenophthalmus*. B, an aggregation of adult *Canthidermis maculatus* in the branches of the same tree; all but three had a dark coloration. C, a group of juvenile *Psenes pacificus*, *Naucrates ductor*, and other carangids beneath a drifting plank; *Psenes* are in a dense clump directly below the plank, *Naucrates* can be recognized by the presence of dark vertical bars. D, juvenile *Canthidermis maculatus*, *Naucrates ductor*, and various juvenile carangids beneath a drifting log.

Divers made daily counts of the number of individuals of each species beneath each of the two logs. The volumes of the two balsa logs calculated from their measurements were 0.021 m.^{3} (log A) and 0.065 m.^{3} (log B).

Counts of the number of individuals beneath logs A and B were 20 and 96 for the second day and 121 and 80 for the third day. By the fourth day it was not possible to make an accurate tabulation because the number of fish under each log was well over 100. On the fifth day 198 individuals were captured under log A and 349 under log B. Prior to being moored log B was encountered 27 miles from shore and 236 fish representing 8 species were captured at that time. Thus more fish were captured after the log was moored 5 days than were collected when the log was drifting 27 miles from shore. Fewer species were represented, however. The larger number of individuals captured beneath log B may reflect the difference in volume of the logs.

Although logs A and B were moored only 100 m. apart, their associated fish populations differed in

species composition, dominant species, and the time at which each species was first observed. No ordered recruitment of species was evident (table 5).

The number of fish collected beneath inflated truck inner tubes varied greatly (table 6). All the tubes were identical in size and shape with the exception of the tube that had 10 manila lines attached. After periods longer than 5 days the number of fish collected beneath the tubes did not increase substantially with time through 20 or more days. The number of fish appears to increase rapidly during the first few days and thereafter to remain at about the same level.

Because a drifting object passes through inshore spawning areas, juveniles of species that spawn inshore would be expected to be more abundant beneath a drifting object than beneath an object moored offshore. *Abudefduf saxatilis* and perhaps *Seriola* sp. spawned inshore. Both species showed a high frequency in the fall collections, but neither was found under the two balsa logs moored in the fall. With these two exceptions, no difference existed in the species composition or in the size of the individuals between populations of fishes associated with moored objects and those associated with drifting objects.

TABLE 5.—*Species recruited to two balsa logs,* A (*volume, 0.021 m.*[3] *and* B (*volume, 0.065 m.*[3]) *moored 100 m. apart 7 nautical miles from the Costa Rican coast in 1963*

Species	Log A		Log B	
	Day species first observed[1]	Fish captured on fifth day	Day species first observed[1]	Fish captured on fifth day
		Number		*Number*
Pseudupeneus grandisquamis	3	87	2	31
Selar crumenophthalmus	3	79	3	304
Caranx caballus	2	17	2	129
Chromis atrilobata	3	8	3	0
Elagatis bipinnulatus	5	6	4	6
Psenes pacificus	–	–	5	2
Blenniolus brevipinnis	5	1	–	–
Caranx marginatus	2	0	4	2
Polydactylus approximans	3	0	3	0
Alutera	–	–	4	0
Total		198		474

[1] No underwater observations were made on the day the log was moored (Day 1).

TABLE 6.—*Number of fish and species recruited to various objects moored near the Costa Rican coast in 1963*

Object	Time elapsed after establishment	Fish	Species	Distance from shore	Season
		Number	*Number*	*Nautical miles*	
Truck inner tube[1]	15 hours	203	6	31	Spring
Balsa log (A)	5 days[2]	198	7	7	Fall
Balsa log (B)	5 days[2]	474	6	7	Do.
Truck inner tube	6 days	263	8	8	Spring
3 feet by 3 feet by ¼ inch plywood	20 days	2	1	2	Fall
Truck inner tube	20 days	13	4	7	Spring
Truck inner tube	28 days	492	7	8	Do.
Truck inner tube	46 days	118	5	9	Do.

[1] Attached to this inner tube were ten ¾-inch (19 mm.) manila lines 10 m. long. All tubes had a volume of 0.286 m.[3]
[2] Established at same time at same locality.

BEHAVIOR

DISTRIBUTION AND FRIGHT BEHAVIOR

When disturbed, nearly all species swam toward the drifting object and maintained a position much closer to it than when undisturbed. The fishes showed this behavior when a school of porpoise, *Stenella grafmani*, passed a log, when four porpoise, *Tursiops* sp., passed nearby, when a school of black skipjack approached a log, and when a shark, *Carcharhinus azureus*, swam beneath a log. The movements of a diver, skiff, and the research vessel also induced this response. The fishes rapidly habituated to the movement of the outboard skiff; after several passes of the skiff near the same log the fear reaction no longer could be evoked.

Most species showed a marked change in behavior when disturbed. *Abudefduf saxatilis* frequently entered holes or crevasses on the surface of the log. The kyphosids moved in and out of holes and swam back and forth rapidly over the log so close to it that their fins almost touched it. Schools of all species became more compact; sometimes individuals that were a part of a diffuse aggregation of several species separated into monotypic schools. For example, when only a few *Chromis atrilobata* were present under undisturbed conditions they remained with the carangids in a loose aggregation, but when frightened they formed a compact monotypic school.

The fear response produced a marked vertical stratification of species beneath the object. Species distributed at various distances from the log, or members of a common loose aggregation, separated into discrete compact groups. If large numbers of fishes were grouped in this manner the distribution usually resembled a cone, the apex of which was at the underside of the object. The base was usually formed by a large group of juvenile *Selar crumenophthalmus* and *Decapterus* sp. The fish were always in this position when the object was approached by the research vessel or the skiff. It was only after the skiff had been near the log for a half hour or longer that the fish lost these more rigid groupings

and strayed from their position directly beneath the log.

When the fish were undisturbed, the conical distribution beneath the log was not apparent, owing to movements in the horizontal plane and the breaking up of groups. The mixed school of *C. caballus*, *C. hippos*, *C. marginatus*, *Elagatis bipinnulatus*, and *Psenes pacificus* broke up into smaller units, and these at times moved at least 15 m. away from the object. Juvenile kyphosids swam 1.5 to 3 m. away from the object but did not range as far as the juvenile carangids. Adult *Canthidermis maculatus* frequently swam beyond the limit of visibility—15 m.—and returned to the object. *Abudefduf saxatilis* and *Blenniolus brevipinnis*, on the other hand, always remained near the object.

The relative vertical position of species usually was maintained under both disturbed and undisturbed conditions. Those species that increased their horizontal range when undisturbed also increased, to a lesser extent, their vertical range of movements. The juvenile kyphosids swam as deep as 1.5 m. below the object; *Pseudupeneus*, *Decapterus*, and *Selar* were observed at a depth of 12 m. (limit of visibility from the surface). Adult *Canthidermis* was the only species whose relative vertical position changed markedly. Under disturbed conditions this species was often among those occupying a position close to the object, but after the disturbance had ceased they ranged from the surface to depths over 12 m. Juvenile *Canthidermis*, on the other hand, occupied the same relative vertical position under disturbed and undisturbed conditions.

Commonly the responses of juvenile fish to a drifting object differed from those of the adult. Adults swam deeper, ranged farther, and appeared beneath the object less frequently than did juveniles. With the exception of adult *Sectator* and *Canthidermis*, they did not always respond to movements of the skiff by moving toward the object as did all the juvenile fishes. It was not possible, therefore, to be certain that adult *Euthynnus lineatus*, *Coryphaena hippurus*, *Caranx caballus*, or *Selar crumenophthalmus* were truly associated with a particular object.

POSITION RELATIVE TO OBJECT AND LATERAL BODY COLORATION

The lateral coloration of the fishes and their position relative to the object were correlated. The species that remained closest to the log were darker than were those that maintained greater distances from the object or associated with the object only intermittently (table 7). For example, *Abudefduf saxatilis*, *Psenes pacificus*, all species of *Caranx*, the kyphosids, *Blenniolus brevipinnis*, and *Lobotes pacificus*, were yellow, brown, or black and remained near the log. On the other hand, *Chromis atrilobata*, brownish above, silvery below, occupied a deeper position, and *Selar crumenophthalmus* and *Decapterus* sp., which were silvery, regularly occupied the

TABLE 7.—*Lateral coloration (live), estimated vertical distribution and aggregation type of certain species associated with flotsam in the offshore waters of Central America in 1963*

Fishes[1]	Lateral coloration (live)	Estimated vertical distance from object[2]	Grouping
Juvenile:			
Blenniolus brevipinnis	Dark brown with black bars	0	Individual
Abudefduf saxatilis	Yellow with dusky bands	0–3	
Canthidermis maculatus	Blue with white spots to black	3	
Polydactylus approximans[3]	Silvery below, blue above	3	Pure school
Kyphosus analogus	Black with pale purple stripes and spots	0–15	Individual
Kyphosus elegans	Black with pale purple stripes and spots		
Sectator ocyurus	Yellow with brown stripes below, dark olive green above		
Caranx caballus	Yellow below, olive above		
Caranx hippos	Yellow with dark dusky bands	15–150	Mixed school
Caranx marginatus	Yellow with dark dusky bands		
Elagatis bipinnulatus	Yellow with two blue stripes below, dark bluegreen above		
Seriola sp.	Yellow with black bands below, dark olive above		
Psenes pacificus	Yellow with brown stripes below, olive above		
Chromis atrilobata	Silvery below, pale brown above	150–200	Pure school
Decapterus sp.	Silvery below, blue above	150–600	Mixed school
Selar crumenophthalmus	Silvery below, blue above		
Pseudupeneus grandisquamis	Silvery below, blue above		
Adult:			
Canthidermis maculatus	Blue with white spots to black	0–300	Pure school
Caranx caballus	Silvery below, blue above	600–1300	

[1] Only those species are included for which we have sufficient notes on vertical distribution.
[2] Estimate made under disturbed conditions.
[3] Did not school beneath log but to one side near the surface.

deepest position of all the permanently associated fishes. This relationship suggests a protective advantage afforded by the log other than the physical obstruction of predators. The dark brown, yellow, and black of the closely associated species was well adapted to the colors of the most commonly occurring flotsam. Thus, when associated with flotsam, the more darkly colored species were probably less conspicious to predators than when isolated. From examination of fishes associated with flotsam in the Atlantic, Murray and Hjort (1912) made similar speculations. They also suggested that *Naucrates ductor*, blue with darker transverse bars, might occupy an intermediate position between the organisms strongly associated with flotsam and those which merely live near drifting objects.

Although both *Canthidermis maculatus* and *Polydactylus approximans* had a pelagic coloration, they were frequently near the object when frightened. The fright reaction of *Polydactylus* differed from that of other species. These fish formed a compact rapidly moving school a few centimeters below the water surface. The school moved about near the object but never below it. Adult *Canthidermis* when undisturbed swam deeper and ranged farther from the object than all the yellow, brown, and black species. When frightened they moved to 0 to 3 m. below the object. Thus, this species occupied a position in keeping with its pelagic coloration only under undisturbed conditions. *Canthidermis* has the ability to turn from the normal pelagic coloration, blue with white spots, to black. Juveniles and adults had intermediate color phases as well as pelagic and dark phases.

Within the same species, coloration appeared to reflect differences in the behavior of association. The silvery adult *C. caballus* did not maintain close contact with an object and appeared beneath it only intermittently. The yellowish juvenile *C. caballus*, on the other hand, maintained close contact with the object. Gooding and Magnuson (see footnote 1) reported that when *Psenes pacificus* was associated with their raft it was yellow, but unassociated individuals were silvery.

FEEDING BEHAVIOR

Adult *Canthidermis*, *Alutera*, and juvenile *Elagatis* frequently were seen feeding on colonial salps. Once we saw three *Canthidermis* nipping the base of the neck and legs of a green turtle. On no other occasion did we see this species engaged in activities that could be interpreted as parasite cleaning. Occasionally juvenile kyphosids were observed snapping at the surface of a log or branch. Juvenile *Abudefduf* showed this behavior more frequently.

Adult *Coryphaena hippurus* frequently pursued smaller fishes located beneath flotsam. We did not see them capture fish, but the stomach of an adult *Coryphaena* taken by hook and line contained a *Caranx caballus*. Frequently fishes with lateral lesions were seen beneath logs. These included *Caranx caballus*, *Canthidermis maculatus*, and *Elagatis bipinnulatus*.

Two schools of skipjack, and one of yellowfin tuna were associated with logs in the study area and were seined by American tuna fishermen. When the boats reached port, stomach contents of fish from each school were examined and the lengths of the fish determined. Euphausiids and myctophids were the dominant food organisms in the stomachs of skipjack, and the portunid crab, *Portunus affinis*, in the stomachs of yellowfin tuna. Only seven stomachs contained fishes—carangids and scombrids—that may have been associated with flotsam (table 8). Stomachs from each of the three schools contained debris of the kind usually found near drifting logs (pieces of wood, thorns, and bird feathers).

TABLE 8.—*Occurrence of flotsam-associated fishes in the stomachs of two schools of oceanic skipjack, and one school of yellowfin tuna associated with flotsam in offshore waters of Central America in 1963*

Stomach contents	*Skipjack* seined October 3, 1963 (222–48)[1]		*Skipjack* seined October 6, 1963 (213–61)[1]		*Yellowfin tuna* seined June 18–22, 1965 (149–107)[1]	
	Number	*Volume Ml.*	*Number*	*Volume Ml.*	*Number*	*Volume Ml.*
Fish						
Flotsam-associated species	0	0	1	77.0	6	575.0
Unassociated species	10	281.1	34	1448.5	7	206.0
Unidentified remains	3	0.3	0	0	44	790.0
Invertebrates	33	212.8	26	25 0	73	1579.0
Bird feathers and plant debris	5	—	2	—	3	—

[1] At left, number examined; at right, number with food.

COURTSHIP BEHAVIOR

No eggs of any kind were found attached to the flotsam. Some species observed near drifting objects were, however, in reproductive condition. Three ripe male black skipjack were captured from a school near a large drifting tree. Underwater observations of these fish revealed a high frequency of wobbling and chasing. This behavior was similar

to that described by Magnuson and Prescott[3] for the reproductive behavior of Pacific bonito, *Sarda chiliensis* (Cuvier).

Nearly all the adult male and female *Canthidermis maculatus* captured in the fall were ripe. On one occasion these fish showed what may have been courtship behavior, but no spawning was observed.

TRANSFER OF FISHES TO OTHER OBJECTS AND HOMING

Some species were attracted to the skiff when it drifted alongside a floating object. Only the fishes that occupied upper positions in the aggregation, such as juvenile *Caranx caballus*, *Psenes pacificus*, *Elagatis bipinnulatus*, *Kyphosus elegans*, and *Sectator ocyurus*, showed this behavior. The more deeply positioned species, *Selar crumenophthalmus*, *Decapterus* sp., *Pseudupeneus grandisquamis*, and *Chromis atrilobata* did not transfer to the skiff. Those species most closely associated with the surface of the object, *Abudefduf saxatilis* and *Blenniolus brevipinnis*, did not transfer unless the original object was removed from the water. Transfers to the skiff were only temporary. The fishes swam beneath the skiff, remained there a few minutes, and then returned to the original object. Movements back and forth from the object to the skiff lasted no longer than 30 minutes; thereafter, the fish remained beneath the original object.

Two attempts were made to transfer the fish population of a log to a 4- by 8-foot (122 cm. by 243 cm.), ¼-inch (6 mm.) thick plywood sheet. A log with a fish population was attached to the plywood sheet 24 hours; then the two objects were separated. During daylight, underwater observations were made while the two objects were attached and after they were parted. At no time did the fishes congregate beneath the plywood sheet. They remained beneath the original object during the 24 hours the objects were attached and after they were separated. The experiment was repeated; this time, 60-cm. sections of unraveled ½-inch (13 mm.) manila line were attached at 10-cm. intervals in three rows to the underside of the plywood. The rope produced a dense mass of filaments. After 2½ hours none of the fishes had transferred from the original log to the plywood, but 1 hour after the plywood was freed from the original object, over 100 *C. caballus* had been recruited to the plywood.

The failure of fishes to form a permanent association with new objects, a skiff or plywood sheet, when already associated with another object suggests that a more familiar object may have a higher valence.

Ten adult *Canthidermis maculatus* were captured, tagged, and released separately; four were released 7.5 m. from their original log, four at 15 m. and two at 30.5 m. One hour and 30 minutes later, three of those released at 7.5 m. and three released at 15 m. had returned. Neither of the fish released at 30.5 m. returned. Conceivably the fish planted at the greatest distance could not see the log. The recapture of fish planted at lesser distances suggested that they may return to their log when it is within visual range.

RUBBING BEHAVIOR

Adults of *Coryphaena hippurus*, *Canthidermis maculatus*, and *Sectator ocyurus* frequently rubbed their dorsal surface or sides against the logs and the skiff. An entire school of adult *Sectator* showed this behavior.

SEA SNAKES

We frequently observed the sea snake, *Pelamis platurus*, swimming near the surface. Often a small school of fish of the genus *Polydactylus* was below a snake. On three occasions the snake was feeding. It began to swim backwards; the schooled fish reversed direction and began swimming with their heads oriented toward the tail of the snake. The snake then captured fish from the school by a rapid thrust of the head and anterior portion of the body, directed either to the side and posteriorly or downward and posteriorly.

Klauber (1935) also observed *P. platurus* feed on fish schooled beneath it.

Klawe (1964) examined the stomachs of 56 *P. platurus* from the eastern tropical Pacific. In the 22 which contained food, *Polydactylus approximans* was the most abundant food, *Pseudupeneus grandisquamis* was second, and Mugilidae third. One individual each of *Selar crumenophthalmus*, *Caranx hippos*, and *Fistularia corneta* also were found. Except for *F. corneta* we captured all of these species beneath flotsam, and there was no difference in size between the fishes we collected and those in the stomachs of sea snakes. Apparently *P. platurus* takes advantage of the habit of some species to congregate beneath flotsam.

[3] John J. Magnuson and John H. Prescott—Courtship, locomotion, feeding, and miscellaneous behavior of Pacific bonito (*Sarda chiliensis*). Manuscript, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

ECOLOGICAL INTERPRETATION

Fishes were recruited rapidly to moored objects. The number beneath objects moored 5 days and the number beneath those moored 20 or more days did not differ. Goose barnacles were attached to all four objects moored 14 days or longer, but they were found on only one drifting object. Thus, all but one of the drifting objects probably had been at sea not longer than 14 days. Rapid recruitment appears to be characteristic of the formation of flotsam-associated fish aggregations. Hardenberg (1950) reported that Indonesian fishermen harvest the fishes beneath their palm frond rafts at intervals of several days. Gooding and Magnuson (see footnote 1) stated that fishes were recruited to their raft minutes after it was set adrift.

Recruitment of fishes followed no particular sequence. Small collections containing only a few fish were not necessarily all of one species. The species composition and order of recruitment of fishes to two balsa logs moored 100 m. apart were dissimilar.

The same species dominated our collections in both fall and spring. Similarities were marked between the families and genera represented in our study area and those reported from other areas (Uchida and Shojima, 1958; Besednov, 1960; Kojima, 1960a; Mansueti, 1963). Juvenile carangids were by far the most important family in terms of abundance, number of species, and dominance. They were also by far the most frequently reported flotsam associate from other areas. Other families of fishes commonly encountered in this study and frequently reported by other authors included the Scombridae, Balistidae, Kyphosidae, and Stromateidae.

The presence of attached invertebrates on floating objects appeared not to influence the occurrence of fish species. The only drifting object that had goose barnacles attached did not have a species composition different from that of objects without the barnacles. Although barnacles were present on each of four objects moored 14 or more days, the species composition of the aggregations of fish did not differ from those of objects moored much shorter periods.

Many of the flotsam-associated fishes were schooling species. We believe that the habit of schooling and of association with drifting materials may be related. Two scombrids, *Katsuwonus pelamis* and *Thunnus albacares*, not only associate with inert materials but also with large sharks and whales, and *T. albacares* is a common associate of porpoise schools (Uda and Tsukushi, 1934; and unpublished logbook records of the Inter-American Tropical Tuna Commission). The carangid, *Naucrates ductor*, known for its association with sharks (Dales, 1957), also was found beneath flotsam in this and in other studies (Murray and Hjort, 1912; Galea, 1961). Many fishes school at times with fish other than their own species. *Katsuwonus pelamis* and *Thunnus albacares* school together (Orange, Schaefer, and Larmie, 1957), and juvenile *Selar crumenophthalmus* and *Decapterus* sp. were observed schooling together in this study. *Trachurus symmetricus* (Ayres), a carangid associate of flotsam in southern California waters, schools with *Scomber japonicus* Houttuyn and *Sardinops sagax* (Jenyns)[4] and associates with jellyfish (Limbaugh, 1955). The tendencies of fishes to associate with living animals other than their own species and to associate with inert drifting materials may be related. Atz (1953) suggested, among other possibilities that an aggregating companion for a schooling fish could represent merely "a simple point of reference for optical fixation". Flotsam could function in this capacity for schooling fishes.

A schooling mechanism cannot explain the presence of all the associated species. Some fishes did not school, and for others alternative mechanisms are equally plausible. Mechanisms postulated by other authors were: attraction to food, negative phototactic response to the shadow of the object, shelter from predators, presence of spawning substrate, and parasite-cleaning symbiosis.

Owing to the infrequent occurrence of flotsam-associated fishes in the stomachs of predators the food hypothesis probably can be eliminated for predacious adults.

For juveniles and nonpiscivorous adult fishes the food hypothesis would not apply, as the drifting materials were usually devoid of attached invertebrates and algae that would provide food. That fishes were attracted because plankton was more visible in the shadow cast by the object also seems unlikely, because the fishes did not remain in the shadow. Furthermore, plywood sheets that cast large shadows were less effective in attracting fish than were objects that produced smaller shadows.

That all the juvenile fishes and adult *Canthidermis maculatus* and *Sectator ocyurus* swam toward and beneath the object when predators appeared, sug-

[4] Unpublished data, Bureau of Commercial Fisheries, La Jolla, California.

gests the association has a selective advantage. This behavior was not, however, a mechanism for the association, because fishes remained near the object in the absence of predators.

Use of the object as a spawning substrate would apply only to adult fishes. Adults, however, represented only a small portion of the total individuals present. Adults of two species, *Euthynnus lineatus* and *Canthidermis maculatus*, were in reproductive condition. *Euthynnus* does not have attached eggs, however (Calkins and Klawe, 1963), and no eggs were found on any of the floating materials.

The cleaning-station hypothesis suggested by Gooding and Magnuson (see footnote 1) could apply only to some of the fishes. *Canthidermis maculatus* alone showed behavior that could possibly be interpreted as cleaning. This species was taken in only 14 of the 70 collections. Except in the collection made farthest from shore, where *Canthidermis* and *Balistes polylepis* were the only species present, no differences in the species composition were evident in the collections that contained *Canthidermis*. Thus, if *Canthidermis* regularly consumes parasites of other fishes the activity does not appear to influence the presence of these fishes.

Artificial reefs established in sandy locations rapidly attract groups of fishes that would not otherwise inhabit these areas (Carlisle et al., 1964). The artificial reef provides the habitat requirements for certain fishes in an otherwise unsuitable area. Similarly, a drifting object may provide a suitable habitat for inshore fishes that have pelagic juvenile stages or that have become displaced from shore. This explanation seems to be plausible for the presence of *Abudefduf saxatilis*, *Blenniolus brevipinnis*, *Balistes polylepis*, and other species. The very restricted size range of *Chromis atrilobata* and *Pseudupeneus grandisquamis* suggests that these species are available for association during a limited period. Many of the *Pseudupeneus* were near the size at which metamorphosis takes place. Approaching metamorphosis was indicated by the slight color changes in some of the individuals and by pronounced changes in coloration after the fish were kept in a shipboard aquarium 34 hours. Possibly large premetamorphic juveniles may be attracted to objects because of changes associated with metamorphosis; for these fish the object may represent an inshore or nonpelagic habitat.

In summary, we found little evidence to support the mechanisms postulated by other authors. We have suggested two mechanisms: (1) fishes are attracted to drifting materials because the object functions as a schooling companion, and (2) for species not adapted to a pelagic life and others undergoing a change from a pelagic to other modes of existence, drifting materials may function as a substitute for a reef or other substrate. In both situations the object may have the same function, that is, provide a visual stimulus in an optical void.

The occurrence of juvenile fishes beneath flotsam was much more frequent than that of adults. That some species, as *Chromis atrilobata*, *Pseudupeneus grandisquamis*, and *Agonostomus monticola*, are pelagic only as juveniles can explain the absence of the adults. Of the species that are pelagic as juveniles and adults, the juveniles were in the vicinity of an object for longer periods and remained closer to the object than did the adults. Owing to their larger size and faster swimming speed, adults are probably less susceptible to predation. Thus, for adult fishes the selective advantage of maintaining a close association with a drifting object may be small. It is also possible that development is accompanied by an increase in the specificity of the responses of schooling fishes to other schooling companions. The valence of flotsam as a schooling object would then be lowered and intermittent association with drifting objects might be expected.

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ANALOG COMPUTER MODELS OF FISH POPULATIONS

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ABSTRACT

A modern analog computer, together with an X–Y plotter,[1] provides a means of constructing useful models of commercially exploited fish populations. The model combined conventional exponential fishing and natural mortality rates with a Gompertz curve of growth in weight. By combination of these rates and curve into a single differential equation, survival curves for successive year classes of fish were generated by the computer and plotted by the plotter. Weights for all year classes present in each season were summed graphically. Recruitment was determined from a stock-recruitment curve, set into a function generator of the computer. Yields for each season were calculated by multiplying stock weight by rate of exploitation and were compared with actual yields to test the validity of the models.

The technique was demonstrated by use of empirical and hypothetical data for the Atlantic cod (*Gadus morhua*). It is generally applicable to fisheries for which good measures of total catch, growth rate, natural and fishing mortality rates, and stock-recruitment relation are available.

It is important to use reasonable values of biological variables in constructing the models because it was not possible to demonstrate beyond doubt that the set of parameters for any given model provides a unique solution.

Compared with other techniques, the analog-graphic approach offers low cost of equipment, moderate computation speed, ready accessibility of equipment, and good visibility of results during computation. It is limited in accuracy (two or three digits) and in scaling requirements.

Fishery biologists have devoted much effort in determining changes in fish populations as they respond to varying degrees of fishing intensity. Because stocks usually cannot be observed and measured directly, it has been necessary to use data of catch and fishing effort and biological data on relatively small samples of the stocks. These records, plus associated data on the environment, have composed most of the working materials of the fishery biologist. Limited to such materials, the fishery biologist has been forced to proceed largely by inference. There has been no alternative. As work became quantitative, inference came to mean statistical or biometric inference, or a combination of both.

One method of quantitative inference is that of simulation or modeling. Using the best empirical data and biological judgment available, the biologist erects hypotheses concerning the additive and subtractive processes affecting the stocks. The former include recruitment, growth, and immigration; the latter, fishing mortality, natural mortality, and emigration. To test the validity of the hypotheses, characteristics of the models based on the hypotheses can be compared with what is known of the real populations. Population models are used for the same purpose as models in ship or power-dam design: experiments are easier, quicker, and cheaper with the model than with the full-scale object. Any tool that will help the biologist in these processes should be valuable. This report describes such a tool in the form of an analog computer technique.

Application of the analog computer as described herein has not, to the best of my knowledge, been made previously. Originality is not claimed, however, for the technique of simulation in general or in

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[1] Trade names referred to in this publication do not imply endorsement of commercial products.

the field of fisheries. Familiar applications outside the field of biology include aircraft and spacecraft design, ballistic studies for military services, and management of systems such as power-generating pools and nuclear reactors. Among biologists, the ecologists especially have made use of simulation. Notable examples include the simulation of ecological systems by digital computer (Garfinkel and Sack, 1964) and by analog devices (Odum, 1960 and Margalef, 1962). In fisheries there have been three general types of simulation: analytical, digital, and analog.

Analytical simulation is the oldest and best known. It is so well known that an extensive review is superfluous here. In it the biologist analytically determines the nature of the mathematical relations controlling population structure and population response to exploitation. He then constructs mathematical models which predict what will occur under certain assumed conditions of the fishery and the environment. Most of the classical contributions to fishery dynamics are of this type. They include the work of such authors as Baranov (1918), Russell (1931), Thompson and Bell (1934), Graham (1935), Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). During the history of the analytical technique the complexity and sophistication of the formulations have generally increased; the work of Beverton and Holt unquestionably represents the highest development in this respect to date.

Some of the above authors have also used digital simulation. Thompson and Bell (1934) arithmetically constructed tables to simulate the catch and catch per unit of effort of the Pacific halibut under constant recruitment and certain assumed rates of growth and mortality. They demonstrated a remarkable correspondence between the values predicted by this method and the observed values for certain periods and areas. Ricker (1958) made somewhat similar calculations based on analytical functions and introduced the additional concept of relation between stock size and rate of recruitment. He expressed catches in terms of "equilibrium yields" which would be obtained when the additive processes affecting the populations just balanced the subtractive ones. An outstanding example of digital simulation of a fish stock is found in Larkin and Hourston (1964).

To my knowledge, only Doi (1957, 1962) has proposed application of the analog computer to fishery dynamics. He set forth mathematical formulations and computer block diagrams and made applications to Japanese fisheries. His formulas are similar to those used here, in general, but differ in detail. He also adapted the Volterra equations to analog treatment of predatory and competitive relations among fish populations.

With some notable exceptions (Ricker, 1958; Larkin and Hourston, 1964; Larkin and Ricker, 1964; International North Pacific Fisheries Commission, 1962), fishery-simulation attempts to date have dealt with equilibrium population conditions. This restriction is understandable in view of the mathematical complexities introduced by varying rates. Such an approach does, however, lead to models which are somewhat unreal compared with their counterparts in nature. For instance the number of recruits annually entering the stocks varies widely. This problem has been treated by considering recruitment constant for short periods (apparently close to the truth for some Pacific halibut stocks during various 8- to 10-year periods between 1918 and 1933) or circumvented by expressing results in terms of "yield per recruit." Likewise, fishing mortality varies with fishing intensity. Any realistic simulation of fished populations over considerable periods requires some provision for changes in recruitment and other vital rates, as can be accomplished on the analog computer. The importance of this problem was recognized by Schaefer and Beverton (1963) who wrote:

> ". . . . the characteristics of the recruitment to marine fish populations—its degree of fluctuation, its relation to stock size and the influence on it of changing environmental conditions—are the key to the interpretation and prediction of the long-term dynamics of a fishery . . ."

and:

> "Actual fisheries are, however, seldom in steady states . . ."

The remainder of this report is devoted to a description of the plan of attack (Platt, 1964—strong inference) used in the analog computer approach. Briefly outlined, this plan is as follows:

1. Formulation of vital rates in a manner suitable for analog solution, thus setting up a hypothesis.
2. Simulation of populations and yields over the period for which observational data are available.
3. Comparison of simulated and observed yields, testing the hypothesis.

4. Acceptance or rejection of the hypothesis. If the agreement of simulated with observed yields is good, the hypothesis is accepted. If it is rejected, a new hypothesis is erected by adjustment of parameters in the analog model, and steps 2 to 4 are repeated until satisfactory fit of simulated to actual yields is either attained or found unattainable.

In practice, the process was never repeated more than a few times, since improvement fell off rapidly. Also, indefinite repetition would be out of keeping with the scientific method.

BASIC FORMULATIONS

For the initial trials of the analog technique, I adopted what seemed the simplest useful model of a fish population. This model includes rate of growth, rates of fishing and natural mortality, and a recruitment-stock relation. It does not take account of immigration, emigration, or environmental effects. Symbols used have been adapted from Holt, Gulland, Taylor and Kurita (1959) in furtherance of their admirable attempt to secure uniformity in the terminology of fishery dynamics. Definitions are as follows:

N_t = Number of recruits surviving at time t.
R = Initial number of recruits to fishable stock for a single year class.
f = Fishing effort.
F = Instantaneous rate of fishing mortality.
q = F/f.
M = Instantaneous rate of natural mortality.
Z = $F + M$.
t = Age of fish in years.
t_r = Age of fish at recruitment to fishable stock.
t_c = Age of fish when first vulnerable to capture by gear in use.
P_t = Weight of all fish of a given year class surviving at time t.
P_{to} = Weight of all fish present at beginning of season.
w_t = Weight of individual fish at time t.
w_∞ = Upper asymptotic limit of w_t.
w_r = Weight of individual recruit at time t_r.
$\hat{Y}$ = Estimated yield of fishable stock in weight, per year.
Y_o = Actual yield of fishable stock in weight, per year, from official statistics.
E = Rate of exploitation, $= \frac{F}{F+M}\left(1 - e^{-(F+M)}\right)$.
i = Subscript referring to individual year classes.

In addition to the above, the following symbols have been adopted for the formulations here:

R_w = Initial weight of recruits to fishable stock for a single year class.
G,g = Constants of Gompertz growth curve.

Because interest in this study is centered on the commercial catch, the model is limited to the fishable sizes and ages of fish. For a year class of fish passing through the fishable stock, numbers of fish surviving may be expressed according to the declining exponential formula, as set forth in Beverton and Holt (1957):

$$N_t = Re^{-(F+M)\ (t-t_r)} \qquad (1)$$

To take account of the growth of individual fish, and to obtain yields in weight for comparison with commercial catches, it is necessary to introduce a formula for weight-at-age. Beverton and Holt employed the von Bertalanffy equation for length-at-age, converting to weight-at-age by means of a cubic length-weight relation. Use of the cubic relation has been shown to lead to considerable error when the real relation between length and weight involves a power of length other than 3 (Paulik and Gales, 1964). Although this difficulty can be overcome by use of the Incomplete Beta Function (Wilimovsky and Wicklund, 1963) in the yield equation, the formulation still is not well adapted to analog computation.

As an alternative to the von Bertalanffy equation, I investigated the characteristics of the equation developed by Benjamin Gompertz. He applied it as an expression of human mortality rates, but various forms of it have since been used as growth curves for both length and weight of animals. Its applicability in this respect was thoroughly discussed by Winsor (1932). In the form used by Weymouth and McMillin (1931), it is seen to be an exponential curve in which the slope declines exponentially. They point out that the *relative* (as opposed to *absolute*) growth of an animal declines with age because of an increasing proportion of inactive material, and other causes. The declining slope of the Gompertz curve is in accord with this phenomenon. Also, it provided a good fit to the empirical data of weight-at-age for several fishes.

Beverton and Holt (1957) rejected the Gompertz curve on the basis that it deals with growth as an additive process only, ignoring the breakdown of protoplasm. The net effect, however, of anabolism and catabolism may well be the kind of declining relative growth described by the Gompertz curve. This curve thus did not appear to be rejected on

biological grounds, and since it was practical for analog computation, I employed it.

It may be noted that growth rates of fish typically decline throughout life and can be represented most simply by a positive instantaneous rate which decreases exponentially with time, as in the Gompertz curve. The relations can be expressed in the following formulas (where G represents the initial exponential growth and g governs the exponential rate of decline):

$$w_t = w_r e^{G} e^{-Ge^{-g(t-t_r)}} \tag{2a}$$

$$w_t = w_r e^{G-Ge^{-g(t-t_r)}} \tag{2b}$$

This formula can be combined with formula (1) to express total weight of survivors at any time. It is of interest, also, that it has an upper asymptote w_∞ similar to the "L_∞" of the von Bertalanffy equation. Thus:

$$\text{as } t \longrightarrow \infty,\ e^{-g(t-t_r)} \longrightarrow 0$$

$$\text{and } e^{-Ge^{-g(t-t_r)}} \longrightarrow 1.00$$

so that $w_t \longrightarrow w_r e,^{G}$ as $t \longrightarrow \infty$ from equation (2a) above. The limiting value of this expression is w_∞. If extended from $w_t = 0$ to $w_t \sim w_\infty$, the Gompertz curve has a point of inflection lacking in the von Bertalanffy curve. This inflection is found in age-weight curves of many fishes. The total weight of survivors from a single year class may be expressed:

$$P_t = w_t N_t \tag{3}$$

Substituting in (3) for w_t and N_t their equivalents in (1) and (2b):

$$P_t = Rw_r e^{[G-Ge^{-g(t-t_r)}]-(F+M)(t-t_r)}$$

Because I dealt with weight rather than number of recruits, I set

$$R_w = Rw_r$$

and obtained as my working equation:

$$P_t = R_w e^{[G-Ge^{-g(t-t_r)}]-(F+M)(t-t_r)} \tag{4}$$

For convenience, clarity, and ready comparability with other work, I have dealt with all relationships so far in algebraic form. Although the computer requires differential equations, the differentiation can be performed on the final equation, (4) above.

THE COMPUTER AND PLOTTER

Since analog machines probably are not familiar to most fishery biologists, a brief description seems in order. Modern analog computers (fig. 1) are electronic and perform operations on voltages. The voltage is made numerically equal (analogous) to variables in the problem (e.g., 1 volt = age of fish of 2 years), and component building blocks on the computer perform mathematical operations. Various blocks perform: (1) algebraic summation, (2) multiplication or division by a constant, (3) multiplication and division of two variables, (4) integration, and (5) generation of nonlinear functions. This last building block makes it possible to produce functions if a graph of the function is available even though the equations describing the graph are unknown.

The analog computer is primarily a device for solving differential equations with time as the independent variable. It, therefore, becomes evident that if a biological process can be expressed as a differential equation, the equation can be mechanized by interconnecting analog computer components corresponding to the mathematical operations.

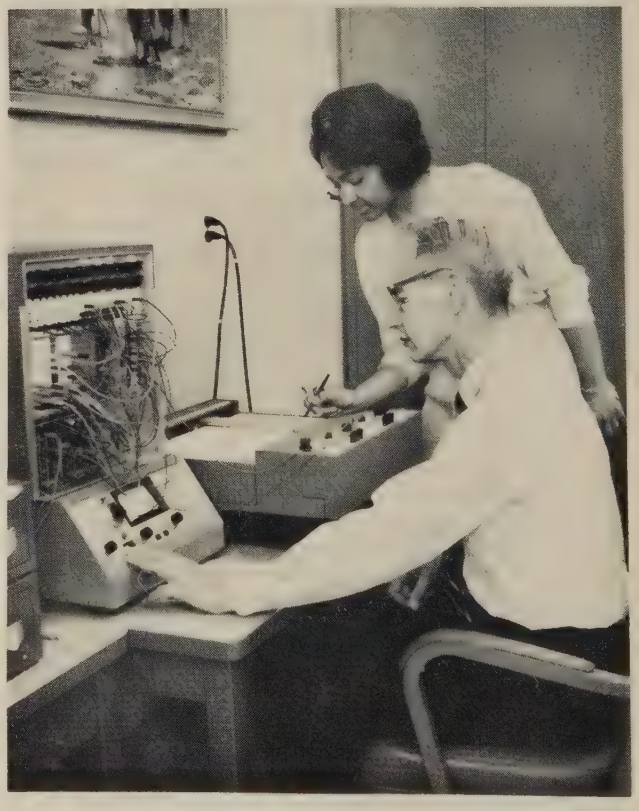


FIGURE 1.—Analog computer and plotter.

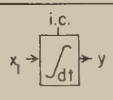
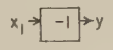
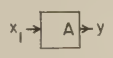
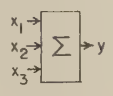
Analog computer programming is based essentially on the electrical principle of the feedback loop. For a simple illustration, let us return to the declining exponential curve, as expressed in equation (1). This expression may be further simplified by setting $F+M=Z$, as in international notation and assuming that our measurement of time begins at t_r so that $t_r=0$ and $(t-t_r)=t$. Expression (1) then becomes:

$$N_t=Re^{-Zt}$$

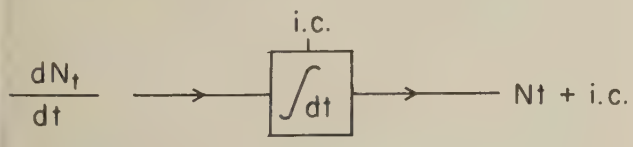
Remembering that the analog computer requires differential expressions, we differentiate the above to find:

$$\frac{dN_t}{dt}=-RZe^{-Zt}$$

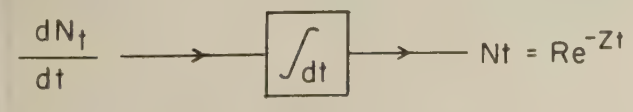
As in digital computation, we start with a "block diagram" (ordinarily this step would be omitted in such a simple circuit, but it is shown here to illustrate the process). A few symbols are needed (arrows indicate direction of information flow):

OPERATION PERFORMED BY COMPUTER	SYMBOL	EQUATION
Integration with respect to time		$y=\int_{x_1}^{t} dt + i.c.$ $i.c.=y]_{t=0}$
Inversion (Change of sign)		$y=-x_1$
Multiplication by a constant		$y=Ax_1$
Summation		$y=x_1+x_2+x_3\ldots$

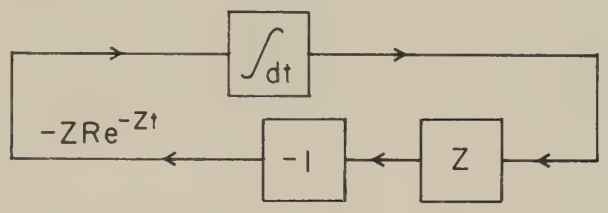
Using the first three of these symbols, we can now construct a block diagram for our differential expression. We start by assuming that a voltage proportional to dN_t/dt exists:



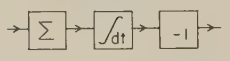
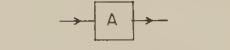
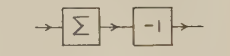
Considering only the rate at which N_t changes, and disregarding its absolute value, we can omit the constant of integration (this constant will be added in the circuit diagram):



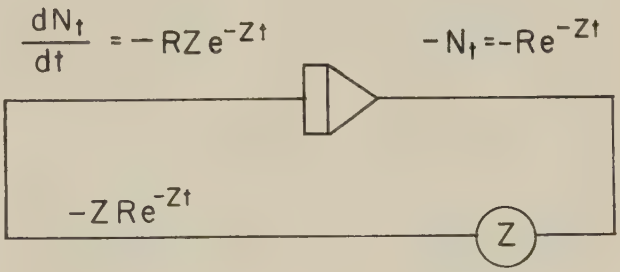
But we know that $\frac{dN_t}{dt}=-RZe^{-Zt}$, so we simply assemble the derivative:



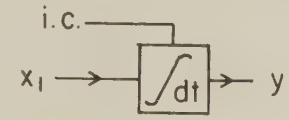
The next step is to construct a circuit diagram showing the actual computing elements and taking account of "initial conditions" and any sign changes that may occur. For this step we use additional symbols:

COMPUTING ELEMENT	SYMBOL	BLOCK DIAGRAM EQUIVALENT
Integrating network with Summing Junction		
Potentiometer		
Summing amplifier		

Still disregarding *i. c.*, we have:

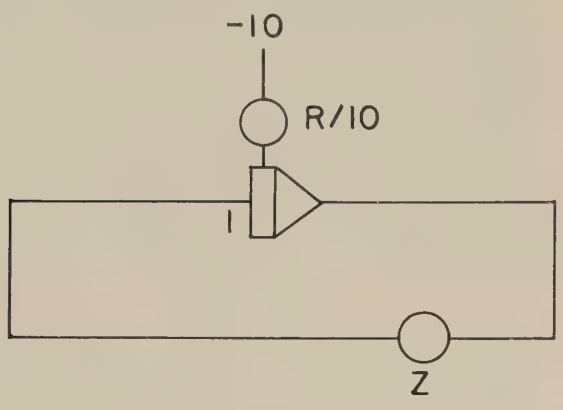


Finally we must supply the "initial condition" voltage, *i.c.*, which is equal to the constant of integration. We noted above, in the definition of the



symbol that $y=\int_0^t x_1 dt+$ *i.c.* and $i.c.=y]_{t=0}$. In our equation "y" is replaced by N_t. Since we set $t_r=0$, by definition $N_t]_{t=0}=R=$ *i.c.* The completed diagram, assuming a computer

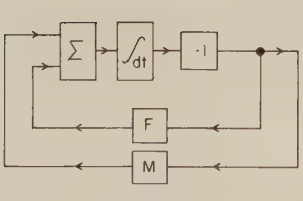
reference voltage supply of −10 volts, becomes:



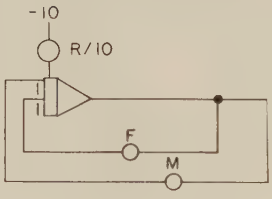
In the operation of the integrating network, *i.c.* only determines the value of N_t (condenser charge) at the beginning of the computation. It is cut off the instant computation begins, and current flow is then confined to the feedback loop. That is why *i.c.* does not appear as a variable in the block diagram. The figure "1" by the integrator input refers to the input resistor. Operation of the integrator is such that the input is multiplied by a factor $100/R_t$ when R_t = input resistance in kilohms.

With the knowledge now at hand we can proceed to set up a circuit in which Z is divided into its components F and M. The equation becomes $N_t = Re^{-(F+M)t}$ and the diagrams are:

BLOCK DIAGRAM



CIRCUIT DIAGRAM



Study of the circuit used here (fig. 2) reveals it to be essentially an elaboration of the basic feedback loop. A multiplier has been added to take care of the nonlinear Gompertz growth curve, and other elements have been added as described in the text. The "time-base" (t) is generated by a simple integrator output. Biologists interested in further information on analog computer programming will find an excellent brief introduction in Strong and Hannauer (1962) or a more extended treatment in Ashley (1963).

The plotter has a pen actuated by two servomotors. One moves it along the "X" axis and the other along the "Y" axis in proportion to an input voltage supplied by the computer. Thus the pen moves to any point X, Y in a system of rectangular coordinates on the plotting surface, corresponding to input voltages V_x and V_y. Since the computer integrates with respect to time, a voltage directly proportional to time is usually fed into "X." The input for "Y" can be taken from any point on the computer circuit to plot the variable(s) desired against time.

As an alternative method of output display, an oscilloscope can be used. This combination requires that the computer be modified for "repetitive operation." Problem solutions are repeated 10 to 100 times per second, so that they appear as curves on the oscilloscope screen. For a permanent record the screen can be photographed as mentioned by Doi (1962).

This oscilloscope display is particularly valuable for curve fitting, since points can be plotted on the face of the tube. In this manner the effect of the potentiometer adjustment in improving the fit is instantly seen.

The work described below was performed on a Pace TR–10 analog computer in conjunction with an EAI Variplotter 1110. The TR–10 is one of the smallest general-purpose analog machines. Since both computer and plotter are fully transistorized, they are small and can be used conveniently atop a desk or small table. The set of units available in the computer as I used it was as follows:

Unit	*Number*
Amplifier (used with integrator, multiplier, etc.)	10
Coefficient potentiometer (used as above)	18
Null potentiometer (used to set coefficient potentiometers)	1
Integrator (used as above)	4
Multiplier (used as above)	1
Diode function generator (use described later in text)	1
Comparator (use described later in text)	1

GENERATION OF SURVIVAL CURVES

The differential equation needed for generating the survival curve of a given weight of recruits, R_w, is obtained by differentiating expression (4):

$$\frac{dP_t}{dt} = R_w e^{[G - Ge^{-g(t-t_r)}] - (F+M)(t-t_r)} [gGe^{-g(t-t_r)} - F - M] \qquad (5)$$

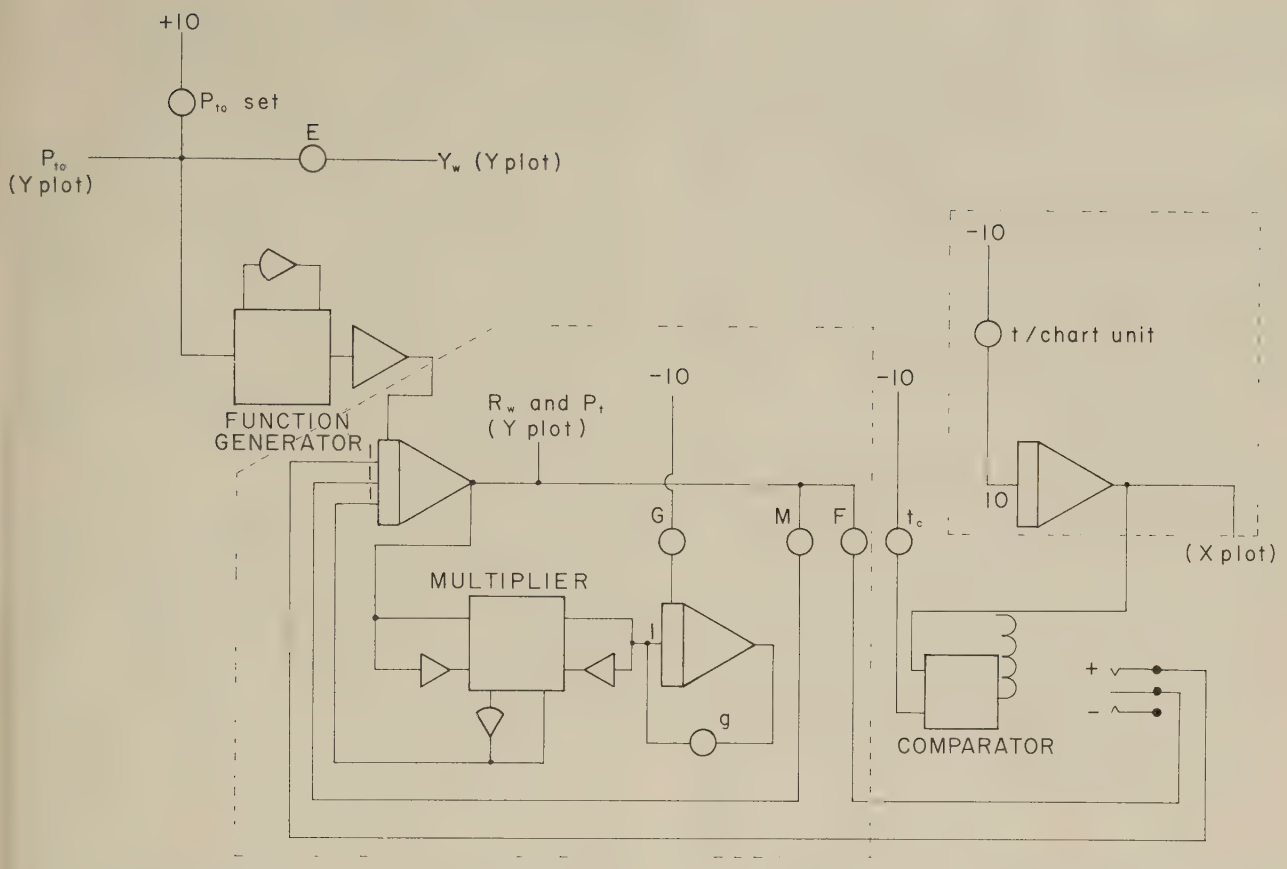


FIGURE 2.—Analog computer circuit for generation of P_t and Y_w. Standard symbols for computing elements, scaling excluded.

By integrating this expression, the computer generates P_t as a function of $(t-t_r)$ for any given values of R_w, g, G, F, and M. The circuit diagram, which includes conventional symbols for the computing elements, is shown within the broken line enclosures of figure 2. The elements outside the broken lines are used in the combination of analog and graphical computation employed to sum the weights of year classes for each season and to determine subsequent recruitment. Their nature and use are described later.

As examples of analog computation, growth and survival curves from the plotter are shown in figures 3 and 4. The data are hypothetical except for the growth constants, which have been derived from data for the California sardine.

Data of growth in weight were obtained by combining a curve of growth in length with a weight-length relation. A table of length-at-age was given in Phillips (1948) and a weight-length relation in Clark (1928). Fitting of the Gompertz relation to these data (fig. 3) was readily accomplished by successive trials, with appropriate adjustment of the potentiometers for G and g. The fitted curve followed expression (2b), with $w_r=93$ g., $G=0.825$, $g=0.445$, and $t_r=2$ years.

Starting with a hypothetical 1,000 fish, $R_w=93$ kg. when $w_r=93$ g. The upper curve (fig. 4) shows how, with no fishing mortality and low natural mortality, P_t may increase for a year or two before mortality overcomes growth. In the two lower curves the effect of adding a substantial fishing mortality may be seen. Application of an increase in fishing mortality at $t-t_r=2$ resulted in the lower branched curve. This change is readily made on the analog computer by placing the machine in the "hold" mode. The potentiometer for "F" is then reset, the machine returned to "operate" mode and the computation resumed. The ability to change quickly the vital rates during a computation is one of the advantages of the analog machine. It may be done even more conveniently by presetting a number of

FIGURE 3.—The Gompertz curve fitted to weight-at-age data for the Pacific sardine following expression (2b) in text; $w_r = 93$ g., $G = 0.825$, $g = 0.445$, and $t_r = 2$ years.

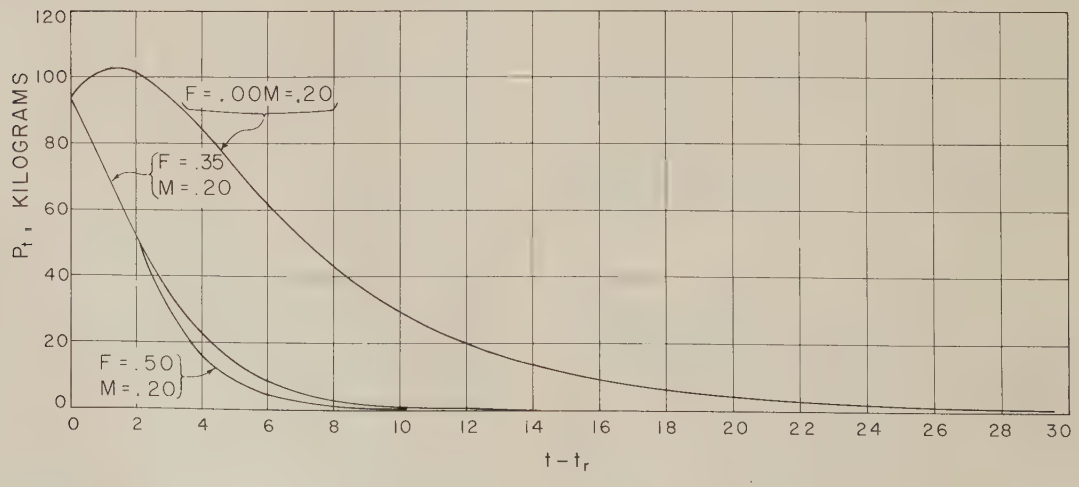


FIGURE 4.—Computer curves of P_t as a function of $(t–t_r)$; growth data from the California sardine, according to expression (4) in text. Values of constants are: $R = 1{,}000$ fish, $w_r = 93$ g., $R_w = 93$ kg., $G = 0.825$, $g = 0.445$.

potentiometers at needed values of "F" and shifting from one to the other.

PROCEDURE OF SIMULATION

Simulation of populations and yields by a combination analog-graphic approach required development of a standardized procedure. A chart was prepared for the plotter, with appropriately scaled coordinates for time (X-axis) and stock (Y-axis). Vertical lines on this chart marked the points for changes in mortality rates or recruitment relation.

Because the commercial stock in any fishing season is made up of survivors from individual year classes of various ages, that stock cannot be started "full blown," with all year classes present. I therefore started with a stock size such that the rate of exploitation (E) estimated to be in effect would produce a catch ($\hat{Y}_w$) equal to the real catch for the first fishing-season, or the mean catch for the first two fishing-seasons of the study period. This stock was then built up by starting year classes at times 1, 2, 3, . . . n years before the beginning of the period; n represents the number of years for a year class to pass through the fishery. During this "prestudy" period, the mortality rates in effect at the beginning of the study period were assumed to be in effect. Each ith curve begins at the value of R_w (assumed the same for each year class) required to produce the specified initial value of total stock $P_{to}=\sum_{i=1}^{i=n} P_{ti}$. This value of R_{wi} can be quickly determined by a few computer trials. P_t for each year class is generated until it declines to a small arbitrary value close to zero, but only the portion extending into the study period is plotted.

The initial and subsequent values of P_{to} are calculated by graphically summing the heights P_{ti} of the ith survival curves for each fishing season, by means of a pair of dividers. Once the initial value of P_{to} has been obtained, the calculation is self-sustaining. From the recruitment curves, values of R_{wi} corresponding to P_{to} t_r years before are obtained. R_{wi} is generated as a function of P_{to} in the Diode Function Generator (fig. 2) by the simple device of setting the P_{to} potentiometer so that the plotter "Y value" corresponds to the P_{to} value for the particular year in question. R_{wi} is then plotted by attaching the Y input to the R_w point in the computer circuit. Any empirical or theoretical curve relating recruitment to spawning stock can be set into the Diode Function Generator, which, with an input x_1, produces an output in the form of a curve $y=f(x_1)$, composed of 10 straight segments.

Survival curves as described above can be generated for each year class entering the fishery during the study period. As in the case of the initial season just described, heights P_{ti} of the individual survival curves for each year are summed graphically, and a mark made representing the total commercial stock, $P_{to}=\sum_{i=o}^{i=n} P_{ti}$. The "$P_{to}$ set" potentiometer is adjusted to bring the "Y-value" of the plotter into conformance with the total stock value P_{to}. The catch is calculated by setting potentiometer "E" (Fig. 2) at the value $E=\frac{F}{F+M}[1-e^{-(F+M)}]$. The catch or yield value proceeds from the simple relation $\hat{Y}_w=EP_{to}$. It is plotted by attaching the "Y input" of the plotter at the point Y_w in the computer. After plotting of $\hat{Y}_w$ the process for R_{wi} (above) is repeated, and the cycle recommenced.

In outline, then, the process of simulating population and yield is as follows:

1. Set the initial value of $\hat{Y}_w$ at the size of the actual catch for the initial year or two of the study period.
2. Determine initial $P_{to}=\sum_{i=o}^{i=n} P_{ti}$ from the relation $P_{to}=\hat{Y}_w/E$.
3. By computer trial, find value R_{wi} such that $\sum_{i=o}^{i=n} P_{ti}=$ initial P_{to}.
4. Generate n curves of P_{ti}, where n is the number of years required for P_{ti} to decline from R_{wi} to an arbitrary small value near zero. Start at 1, 2, 3, . . . n years before the beginning of the study period.
5. By Diode Function Generator evaluate R_{wi} for each season from P_{to} for season t_r years before. Generate curves P_{ti} starting at $P_{ti}=R_{wi}$ for each fishing season.
6. For each fishing season, graphically determine $P_{to}=\sum_{i=1}^{i=n} P_{ti}$. Calculate $\hat{Y}_w=EP_{to}$.

7. Repeat cycle to end of study period, starting each cycle with step No. 5.

EXAMPLE OF APPLICATION

Since hypothetical data are seldom satisfactory to demonstrate the application of a technique, the following example of application to the fishery for Atlantic cod (*Gadus morhua*) is included. It has been used to achieve concreteness, not to make new discoveries about the cod. Catch data were summed for International Commission for the Northwest Atlantic Fisheries Divisions 5Y and 5Z, and the following parameters were assembled for analog computation:

1. The central value of $F=0.35$ used in Beverton and Hodder (1962) was assumed to be the average ($\bar{F}$) for the entire study period 1932–1958. From this figure, values were calculated for eight periods, from the relation $F=qf$, where f was value of fishing effort from Beverton and Hodder and $q=F/f$:

Period	Mean effort thousands of boat-days	$F=qf$, holding mean $Z=0.55$ for: $M=0.2$ (Trials 1 and 2)	$F=qf$, holding mean $Z=0.55$ for: $M=0.25$ (Trial 3)
1932–33	2.00	0.36	0.31
1934–36	1.13	.20	.18
1937–38	2.00	.36	.31
1939–41	2.77	.50	.43
1942 only	1.80	.32	.28
1943–46	1.22	.22	.19
1947–48	1.80	.32	.28
1949–58	2.24	.40	.35

2. The central value $M=0.2$ given by Beverton and Hodder was assumed to be in effect during the entire study period.
3. Lengths-at-age were obtained from Schroeder (1930) and converted to weights-at-age with a length-weight curve fitted to data given in Bigelow and Schroeder (1953). A Gompertz curve was fitted to the weights-at-age with constants $G=1.47$, $g=0.340$, and $w_r=5.9$ lb.
4. No empirical data were available as the basis of a stock-recruitment curve. After some preliminary experimentation, a hypothetical curve (fig. 5A), with mode at an arbitrary $R_{wi}=32{,}000$ metric tons, was adopted for the first formal trial. The concavity of the left hand limb was based only on experience from other species. From data on age composition in Beverton and Hodder it was estimated that $t_r=4$ years.
5. From data in Beverton and Hodder (1962) and Silliman and Wise (1961), it was estimated that if $t_c=t_r$ before the change in cod-end mesh size from 2⅞ to 4½ inches in 1954, then $t_c=t_r+0.25$ year for 1954 and thereafter. This change was accomplished by the comparator (fig. 2), a device which actuates a switch when the input (t in this application) reaches a predetermined value (t_c here). The comparator delayed application of F for one quarter of a year, for year classes entering in 1954–58.

The initial trial simulation, based on the parameters just listed, produced a poor fit of calculated ($\hat{Y}_w$) to actual (Y_w) catches ($r=-0.17$). On the basis of this trial, the shape of the recruitment curve was altered somewhat (fig. 5B) for the second trial. All other parameters remained the same. After the recruitment relation was revised, a second trial produced a considerably improved fit ($r=0.59$). Finally, the value of M was changed to 0.25 and mean F to

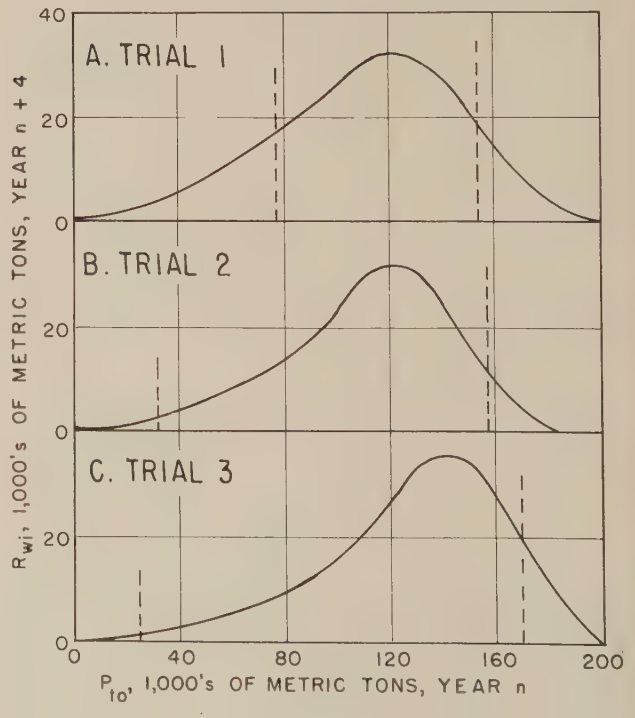


FIGURE 5.—Hypothetical recruitment curves for New England cod. Vertical broken lines indicate range of values used in computations.

0.30, so that $F+M$ remained 0.55. A further adjustment was also made in the recruitment curve (fig. 5C). The third trial, in which these adjustments were employed, yielded a further improvement in the fit ($r=0.69$), which is shown in figure 6. A notable feature of the trials was the sensitivity of the fits to changes in the stock-recruitment relation. The greatest improvement in fit occurred between the first two trials, as the result solely of a moderate change in the shape of the recruit curve (figs. 5A, 5B).

The series $\hat{Y}_w$ and Y_w are not, of course, completely independent, since Y_w enters to some extent into the calculation of the parameters used to compute $\hat{Y}_w$. As a relative measure of goodness of fit, however, the coefficient is of some value. It is possible to make at least two positive statements regarding r as used here:

1. If the calculated P value is greater than the significance level, the real value is certainly greater. Additional degrees of freedom will be lost according to the degree of dependence of the variables. It is possible, then, to identify markedly nonsignificant fits.
2. For calculated correlations within conventional significance levels, the value of r serves as a means of comparing two fits. If one set of parameters generates a fit with a higher value of r than another, then it should be closer to the truth than the other.

The parameters used in the simulations have varying and subtle degrees of dependency on the catch data. Thus, to assess accurately the value of P for the coefficients would require a lengthy and complicated statistical analysis. This work appears hardly to be warranted in view of the approximate nature of the simulations.

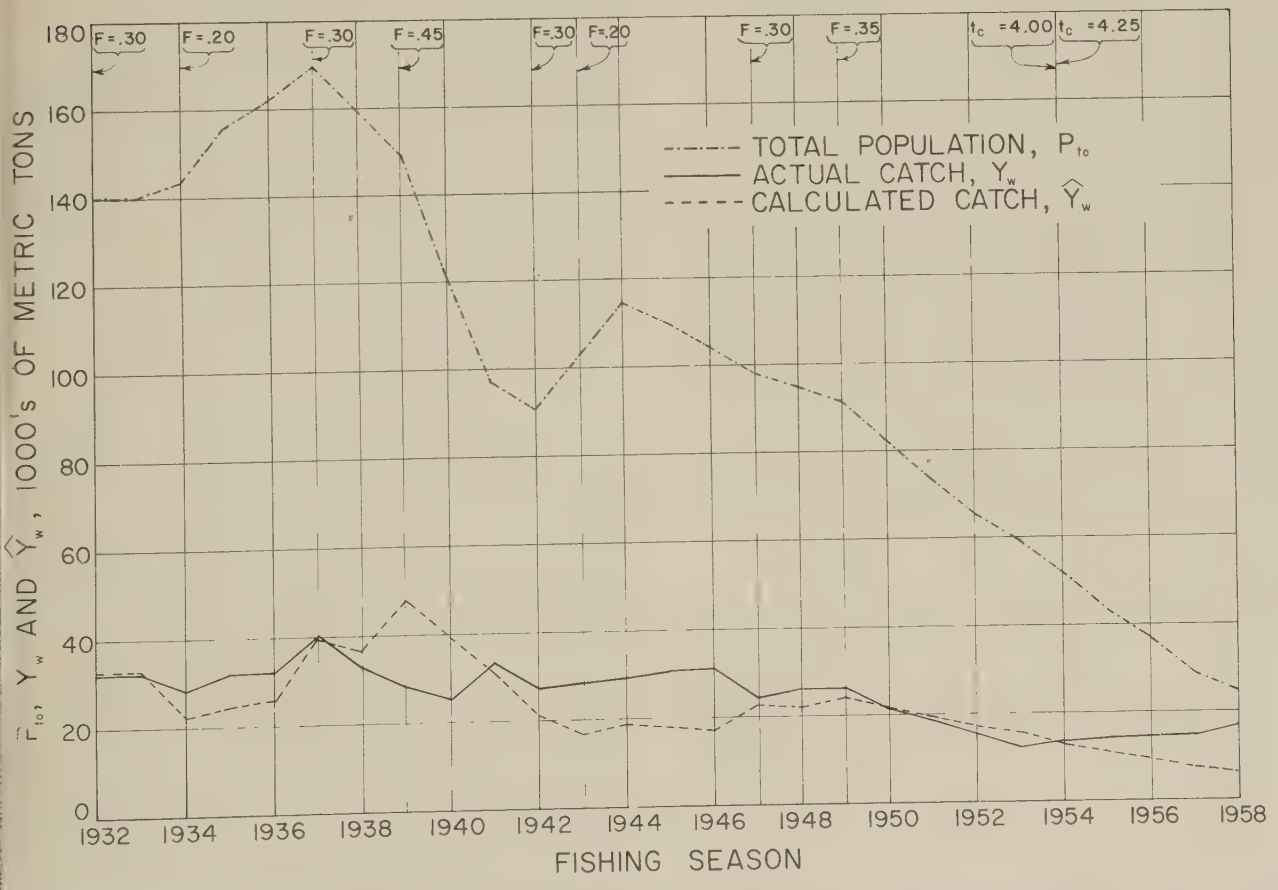


FIGURE 6.—Population and yield simulation for New England cod; $M = 0.25$, $G = 1.47$, and $g = 0.34$ for entire period. Other parameters as shown in drawing.

GENERAL APPLICATION OF THE TECHNIQUE

Application of the analog computer technique described in this report requires estimation of a series of constants or parameters. It also requires a number of approximations and some appraisal of their uniqueness. These two topics will be discussed in this section.

PRELIMINARY ESTIMATES OF PARAMETERS

An extensive literature is available on the estimation of parameters of fish populations under exploitation. The most thoroughgoing summaries and descriptions known to me are given in Beverton and Holt (1957) and Ricker (1958). Treatment here is limited to the specific constants, variables, and relations which must be estimated for simulations by analog computer as described above. They will be considered in descending order of the degree of certainty with which they are likely to be known.

1. Annual yield. For most commercial fisheries this figure is likely to be known rather precisely. Since the original data come from weighouts at the time the fish are first sold, their accuracy has been watched closely by both fishermen and fish buyers. If possible, catches should be segregated according to biological stock units.

2. Growth in weight. Lengths or weights at specific ages are among the most commonly gathered fishery data. If data are in lengths, they must be converted to weights through a length-weight curve. The length-weight relation is fairly stable as compared with other parameters and can be determined from a relatively small number of samples covering the size range of the fish in question. The Gompertz growth curve can be fitted to the empirical data directly on the analog computer simply by adjusting potentiometer settings for G and g until a good fit is obtained.

3. Instantaneous fishing mortality rate, F. This rate may be difficult to estimate with accuracy. If empirical estimates are lacking, however, it may be possible to produce an "educated guess" through general knowledge of the history of the fishery, its changes in yield, the size of the current fishery, ... This value can be adjusted during simulation.

Once a value of F is available for one period, the values for other periods can be estimated if fishing intensity is known. Data on the number and size of units in the fleet are usually available. These figures must be multiplied by an estimate of time in operation to obtain the value of fishing effort, f. Once a series of values of f is on hand, together with F and f for a "base period," values of F for all periods can be calculated from the relation $F=qf$, where q is a constant to be determined from the base-period data.

4. Instantaneous natural mortality rate, M. Estimates of M may be available from tagging or biological data, or an assumed value may be selected for the initial trial. If an assumed value must be used, guidance can often be obtained from the growth characteristics of the fish (Beverton and Holt, 1959; Beverton, 1963). For fish in the commercially available stock, values of M are often low, in the vicinity of 0.1 to 0.3. Frequently, reasonable approximations can be obtained by considering M to be constant during the study period, for all ages of fish.

5. Stock-recruitment relation. Of the items required for simulation, this one is usually the most difficult to obtain. If data are available on age composition, it may be possible to estimate the abundance of the youngest (or youngest important) year class in the commercially available stock. A series of such estimates can then be related to the estimated size of the spawning stock t_r years earlier, as was done by Clark and Marr (1955). The resulting scatter diagram may reveal a pattern that can form the basis for one or more recruitment curves. It is significant that only the portion of the curve covering the stock sizes encountered can affect the outcome of the simulation.

SUCCESSIVE APPROXIMATIONS AND UNIQUENESS

Once the preliminary estimates of the parameters are assembled, simulation trials can begin. Because all the work is visible on the computer chart as it proceeds, it is often possible to see in what direction the parameters must be changed to produce a better fit of calculated to actual catches. Experimentation is readily accomplished, since all parameters may be changed simply by resetting potentiometers (either coefficient potentiometers or the several small ones in the Diode Function Generator). For trials in the applications above, each trial for 26 or 27 fishing seasons consumed about one-half day. This work included preparation of the chart and all other necessary operations leading to a plot of annual populations and yields. It is thus possible to accomplish several trials within a reasonable period of time.

In any trial-and-error approach involving several variables, the question of uniqueness must be faced. It is fair to ask, if one set of parameters has produced a reasonable result, may not another set produce one that is equally reasonable?

Although it is not possible to answer the above question for the general case, some light may appear from a further examination of the trials on cod reported above. In assessing goodness of fit, I took account of the ratio of mean heights of the calculated and actual catch curves, as well as the correlation between them. Thus I had two criteria of "goodness of fit": $\bar{\hat{Y}}_w/\bar{Y}_w$ and r. To provide some idea of the discriminative value of these criteria, I made additional simulations in which only F or M was varied and all other parameters were held constant. Curves of calculated values (fig. 7), bracketing those used in the third trial above, are revealing. For this particular set of combinations, only one other than the third approaches its "goodness of fit." The combination of $F=0.35$ with $M=0.25$ produced about as good a fit as the combination of the third trial; r was slightly higher, and $\bar{\hat{Y}}_w/\bar{Y}_w$ was slightly lower. The difference in F of 0.05, however, is well within what might be considered reasonable error in a rough approximation.

Obviously, curves of the type in figure 7 cannot "prove" the uniqueness of fit obtained with any particular combination of parameters. Since F, M, and the shape and height of the recruitment curve can be continuously varied, the number of possible combinations is infinite. Every effort should be made, therefore, to use reasonable values of biological parameters. Thus we know that F, M, and the recruitment curve are sound because biologists generally recognize that fish stocks are affected by fishing, natural mortality, and recruitment. The question of "reasonable values" is more difficult, but the range of possibilities may be narrowed by use of empirical data as indicated under "Preliminary Estimates of Parameters."

COMPARISON WITH OTHER TECHNIQUES

By appropriate transformations of the formulas, any of the calculations reported above can be performed on either conventional desk calculators or electronic digital computers. It is pertinent, therefore, to consider the relative advantages and disadvantages of analog computation as compared with other techniques.

1. *Initial cost of equipment.*—The analog computer and plotter equipped as I used them cost about $8,000. This figure is substantially more than a good desk calculator ($1,000 to $2,000) but not over one-tenth the cost of comparable digital equip-

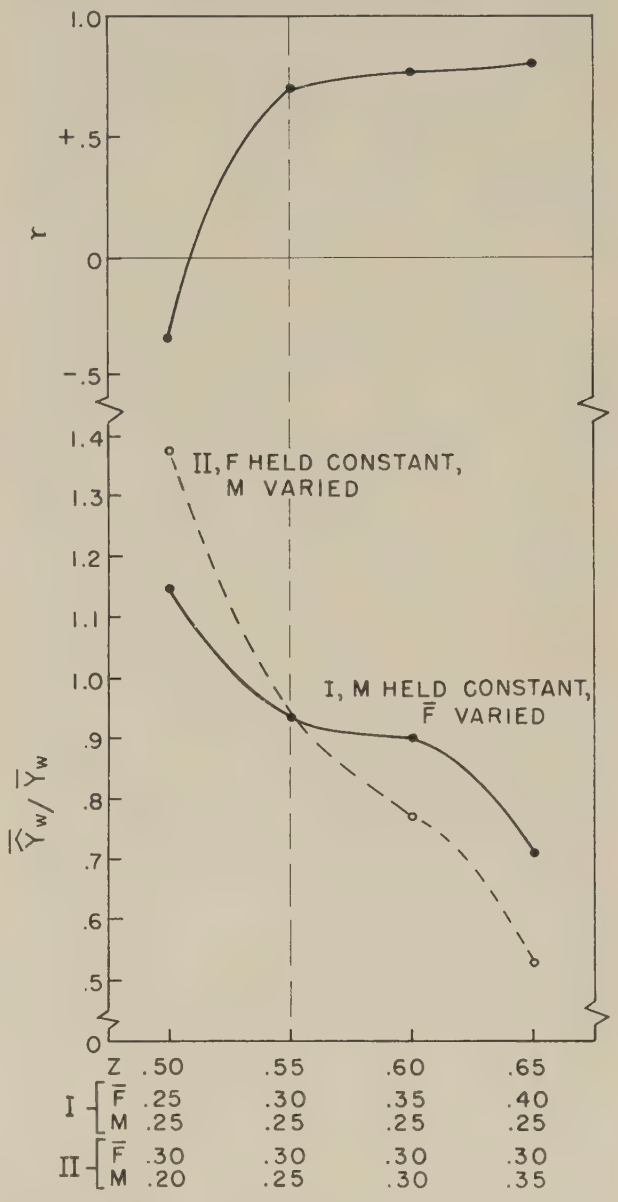


FIGURE 7.—Effect of varying F or M in simulation trials with cod. The value r is the coefficient of correlation between calculated catches ($\hat{Y}_w$) and actual catches (Y_w). Since r is affected only by Z, and not the ratio of its components F and M, it has only one value for each pair of combinations. The fraction $\bar{\hat{Y}}_w/\bar{Y}_w$ represents the ratio of the mean calculated catch ($\bar{\hat{Y}}_w$) to the mean actual catch ($\bar{Y}_w$). Vertical line of dashes indicates combination of values used in third cod simulation trial.

ment. It is, of course, possible to perform work on digital machines under contract or rental arrangements at no initial cost. This arrangement is also possible for analog machines.

2. *Time required for computation.*—For the total operation as outlined above, limited tests indicated analog-graphic computation to be about four times as fast as desk calculation. With digital computers, the calculation time is a matter of minutes. If time required for preparation of data for computer calculation, programming the computer, and exchange of data with the computer center are considered, however, total time may well approach that for the analog method.

3. *Visibility of work during computation.*—In the analog-graphic method, stock size, recruitment rate, and yield are all visible in graphic form as the computation proceeds. This advantage is important to the biologist, since it quickly reveals absurd results, or permits him to end a computation that is leading away from reality. Work is invisible during digital computation, and the final "readout" is usually in the form of a table that may have to be plotted for study.

4. *Scale adjustment.*—Quantities generated within an analog computer must be kept within the voltage limits of the machine. This limitation leads to a considerable amount of "fussing" to achieve proper scaling of the variables. This problem is only minor in digital calculation and therefore represents a comparative disadvantage for the analog computer. Fortunately, once scaling has been adopted for a given formula, it can usually be used with only one or two changes when shifting to a new set of empirical data for the same formula.

5. *Accuracy of results.*—Because of the nature of components in an analog computer, the final results are usually accurate only to two or three significant digits. At the present stage of development of fishery science, the empirical data available are not such as to justify carrying more digits. In fact, two-digit accuracy in fishery predictions would be considered more than satisfactory by most fishery administrators. Thus, the accuracy limitations of the analog machine as compared with digital computation do not at present represent a serious disadvantage.

6. *Summary comparison of methods.*—From the above brief listing, the analog technique is seen to have advantages in comparatively low initial cost of equipment, moderately rapid computation rate, and visibility of results. It has limitations in accuracy and in scaling requirements and is slower than a digital computer. Decision as to which technique to use must depend on the situation of the individual investigator. Factors bearing on the decision include the salaries of persons doing various parts of the work, the accessibility of the research station to a digital computer, and the types of empirical data available.

UTILITY OF THE TECHNIQUE

In this report I have described what may be a useful working tool for the fishery biologist. The example of application given demonstrated the types of basic data needed and the way in which they could be adjusted to improve "goodness of fit" of calculated to actual catches. As with any technique, its utility can be assessed only by those making use of it.

Where extensive biological data are available, simulation is valuable in determining the effects of interaction among the varying mortality, growth, and recruitment rates. The accuracy with which actual catches can be reproduced should serve as a check on the validity of the sampling, analysis, and interpretation involved in the derivation of population parameters.

SUMMARY

1. The objective of this study was to develop an analog-computer simulation technique for modeling exploited fish populations.

2. The mathematical formula for survival of a year class expressed the effect of fishing and natural mortality rates and incorporated a Gompertz curve of growth.

3. Survival curves for successive year classes were generated on an analog computer through use of the differential form of the survival formula. A combined analog-graphic technique summed the weights of survivors in each season to give the weight of the fishable stock.

4. Yield was calculated by applying the rate of exploitation to the fishable stock.

5. Properly lagged recruitment was determined from the stock weight through a stock-recruitment curve.

6. Mechanics of the technique were demonstrated by application to the Atlantic cod.

7. This technique may be applied to any fishery for which good measures or estimates of catch,

growth rate, fishing and natural mortality, and stock-recruitment relation can be obtained.

8. The problem of uniqueness was studied from simulations in which F and M were varied over a range of values. The failure of results to prove uniqueness brings out the importance of using reasonable values of parameters.

9. As compared with other techniques, the analog-graphic approach described here offers low initial cost of equipment, moderate computation speed, ready accessibility of equipment, and good visibility of results during computation. It has limitations in accuracy (two or three digits) and in requirements for scaling variables.

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A SEROLOGICALLY DETECTED SERUM FACTOR ASSOCIATED WITH MATURITY IN ENGLISH SOLE, *PAROPHRYS VETULUS*, AND PACIFIC HALIBUT, *HIPPOGLOSSUS STENOLEPIS* [1]

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ABSTRACT

An antigenic serum component in maturing female pleuronectids was detected by immunodiffusion techniques. Its presence was related to age, length, and maturity in English sole (*Parophrys vetulus*) and Pacific halibut (*Hippoglossus stenolepis*). The factor had a qualitative seasonal variation for English sole; the highest incidence was during the spawning season and the lowest at midsummer. The factor was detected in all mature female halibut sampled, but complete seasonal data are lacking for this species because samples were not available in summer and fall. The factor was detected in the serum of some immature females of both species during the spawning season. Evidence associating the synthesis of this factor with the production of estrogenic hormones was obtained when estradiol was injected into male English sole and induced them to produce the factor.

Maturity studies are an important aspect of biological investigations of fish. Knowledge of age and size at maturity, fecundity, and duration and frequency of spawning is generally required in the management of a species. As a result of the importance of information on maturity, a wealth of literature exists on the subject covering a broad range of fish species. Most maturity investigations have been concerned with development of ovaries rather than testes because of the importance of egg production in population dynamics.

Biological studies of maturity of the Pleuronectidae (flounders) are representative of the variety of approaches for fish generally. Pleuronectid ovaries may be easily classified as developing or immature by macroscopic inspection during the intervals before and after (and including) the spawning season. Harry (1959) used this method to study time of spawning, length at maturity, and fecundity in three species of flounders. Use of a maturity scale, devised by Heincke (1898) for North Sea herring investigations, allows more quantitative estimates of annual ovarian variations. To calculate the spawning season of the Dover sole (*Microstomus pacificus*) Hagerman (1952) used a typical modification of Heincke's scale, based on grossly discernible criteria such as size, transparency, and presence of macroscopic ova. More precise information can be gained by examining the interior of the ovary. By microscopic study of egg diameter and the development of ova, Thompson (1915) determined the presence of egg stocks for more than one season in the Pacific halibut (*Hippoglossus stenolepis*) and found an extended spawning interval for individual females. Through histological methods, Franz (1910) identified four distinct developmental stages and established a firmer understanding of the maturity process than could be done solely by external observations of the ovary in plaice (*Pleuronectes platessa*).

Characteristic changes in the blood of certain

[1] This material was included in a thesis submitted by Mr. Utter in partial fulfillment of the requirements for the M.S. degree from the Graduate School of the University of Washington.

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female vertebrates are related to maturity and can be studied by biochemical and serological techniques. Serum vitellin has been associated with maturation in hens (Roepke and Hughes, 1935) and related serologically to egg vitellin in fowl (Roepke and Bushnell, 1936). Analogous conditions have been described in other oviparous vertebrate classes including teleosts. Uhlenhuth and Kodama (1914), as quoted by Sasaki (1932), used antisera prepared from carp ovaries to distinguish serum of mature female carp from serum of immature female and male carp. Ridgway associated a serologically detected serum factor of the sockeye salmon (also found at high concentrations in the egg) with maturity in females (Ridgway, Klontz, and Matsumoto, 1962); subsequently he has found the antiserum to cross-react with mature females in all salmonid species tested (Ridgway, unpublished data). Concurrently, Vanstone and Ho (1961), in studies of electrophoretic patterns of coho salmon sera at various stages of development, observed a component that was characteristic of maturing females. Fine and Drilhon (1963) identified a similar protein in *Salmo salar* by immunodiffusion. Existing evidence indicates that serum vitellin may be accounted for by the following sequence of events in oviparous vertebrates: under the control of the pituitary, estrogen produced in the ovary stimulates production by the liver of proteins that are passed through the blood to the ovary and there utilized in yolk formation.

The present study attempts to unite the biological and serological approaches in investigations of the maturity of two pleuronected species. We originally intended to study only Pacific halibut. When we found that collecting an adequate halibut sample was impractical, we included English sole (*Parophrys vetulus*), a more available species. The study is based on a serum-vitellin component, called the HM factor, which occurs in mature female flounders. The objective is to demonstrate that serological methods may be advantageously applied in maturity studies of these species by showing the relation of the factor to various biological features.

METHODS AND MATERIALS

The serological methods, preparation of the antigenic substance used in the methods, and the collection of samples for analysis as well as for determination of age of fish from which samples were taken are described.

SEROLOGICAL METHODS

The procedure for the detection of the HM factor was a microslide adaptation of the Ouchterlony method of double-diffusion precipitin analysis as described by Ridgway et al. (1962). The diffusion method provides a means of identifying antigenic components of a solution through diffusion of the solution and an antiserum towards one another in a semisolid medium.[3] If the antiserum contains antibodies specific for components of the solution, a precipitate line is formed in the zone where given antigen molecules meet specific antibodies in optimal proportions. If two antigen solutions that are placed adjacently diffuse towards a single antiserum source, precipitate lines for common antigen-antibody systems will fuse.

Tests for the presence of the HM factor were made in the manner illustrated in figure 1. Sera from known HM-positive females were placed in positions 1 and 4, thus placing each unknown serum adjacent to an HM-positive individual. Distinct positive reactions are seen in positions 5 and 6; a weak positive reaction in position 2, and no reaction in position 3. This arrangement was particularly useful for positive individuals with low concentrations of HM antigen. Although a distinct line was not necessarily formed, a bending of the control line towards the unknown position, as in position 2, indicated the presence of the HM factor and allowed a highly sensitive test for the HM factor's presence.

Relative concentrations of the HM factor were determined by a single-diffusion method described by Hayward and Augustin (1957). In this method the antiserum is incorporated into the agar at 5 percent concentration and serial dilutions of the fluid bearing the HM factor are introduced into wells in the agar. The end point, the highest dilution at which a visible ring can be observed around the well, is referred to as the titer of the solution for the HM factor. Figure 2 illustrates the reactions of serial dilutions of HM factor from an extract from eggs of starry flounder (*Platichtys stellatus*) with the antiserum used in this study. (The preparation of both the extract and the antiserum is described below.) The end point is at the 1/160 dilution.

[3] The medium in this study had the following composition: Difco agar, 1.5 percent; sodium chloride, 0.72 percent; sodium citrate, 0.6 percent; merthiolate, 0.01 percent; trypan blue, 0.01 percent. The pH was adjusted to 6.7.

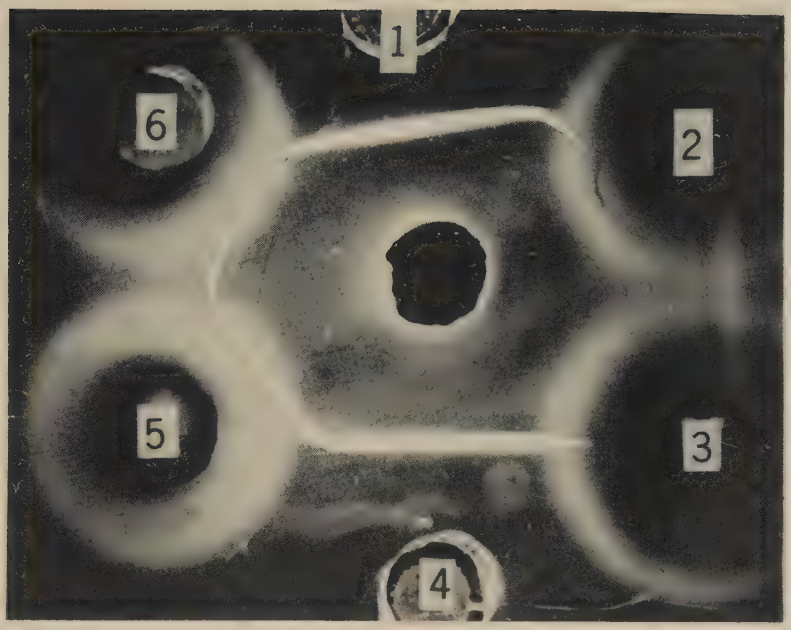

FIGURE 1.—Reactions on typical double-diffusion slide demonstrating tests for presence of HM antigen in kidney-tissue fluids of female English sole. Magnification 5X.

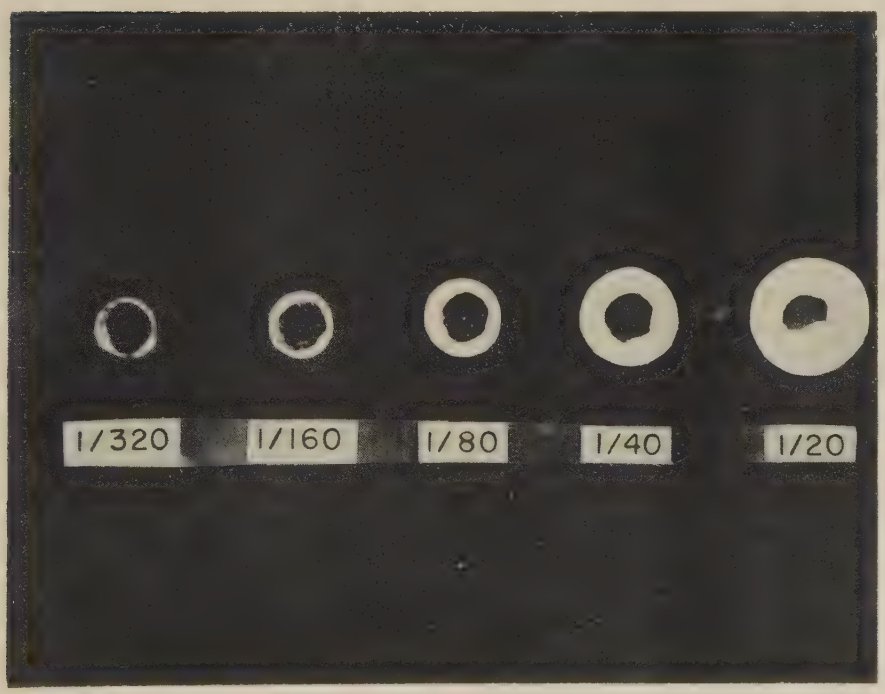

FIGURE 2.—Demonstration of single-diffusion technique to estimate relative concentrations of HM antigen. End point is seen at 1/160 dilution. Magnification 2.5X.

PRODUCTION OF ANTISERUM

The antigenic substance used for production of antisera was a vitellin preparation from starry flounder eggs. This preparation met the classical biochemical criterion for vitellin, since it was the water-insoluble fraction of the egg yolk (Jukes and Kay, 1932). The preparation was made in the following manner: extraction was in a Waring Blendor [4] from 1 part of eggs to 3 parts 1 percent saline solution. One part of the supernatant obtained after centrifugation at 10,000 r.p.m. for 20 minutes was diluted with 11 parts distilled water, and the resulting precipitate was dissolved in 1 percent saline, reprecipitated, and redissolved. The vitellin preparation was utilized in this final form for immunization procedures. Although different injection routes were used and the vitellin preparation was injected both with and without adjuvants, consistently uniform antisera were produced in the five rabbits that were stimulated. Because of this uniformity, a single pooled reagent composed of numerous bleedings from all of the rabbits was made and used throughout this study.

The antibody specificities appeared to be directed toward one or more of the starry flounder's vitellin antigens. The pooled antiserum cross-reacted with serum of mature females of all pleuronectid species tested. Reactions with sera from males were observed only infrequently. These reactions were invariably weak and are discussed in a later section.

COLLECTION OF SAMPLES

Collection dates and numbers of English sole sampled are listed in table 1. All samples were collected by the University of Washington research vessel *Commando* at the Port Orchard area of Puget Sound. Only female English sole were taken. These fish, with the exception of the March sample, were randomly sampled over a variety of lengths. This sample was biased toward smaller individuals with relatively undeveloped ovaries. This bias was based on the relatively high frequency of the HM factor in smaller females in the two previously collected samples; the data for the March sample reflect this bias. Random sampling was resumed through the remainder of the investigation.

Collection of an adequate blood sample from English sole was found impractical, and all qualitative determinations for the HM factor were made from the fluids expressed from kidney tissue. When quantitative data were required, blood samples were collected from larger individuals by cardiac puncture.

The collection data for the halibut samples are presented in table 2. A sufficient blood volume was available from the individual halibut to use serum for determination of the HM factor, although parallel samples of kidney tissue were collected from most fish. All samples were collected under the direction of the International Pacific Halibut Commission.

TABLE 1.—*Collection dates and number of female English sole in samples, Port Orchard area, Wash.*

Collection date	Fish	Collection date	Fish
1962	*Number*	*1963*	*Number*
Dec. 27	30	July 3	25
1963			
Feb. 5	38	July 23	41
Mar. 7	63	October 22	55
June 4	42	November 23	58

TABLE 2.—*Date and areas of collection, number of individual samples, and source of HM antigen for halibut*

Collection date	Area	Fish		Source of HM antigen	
		Female	Male	Serum	Kidney
1960		*Number*	*Number*		
Mar. 25	Queen Charlotte Sound	27	13	x	—
1962					
May 11	Cape Flattery	6	10	x	x
June 6[1]	Queen Charlotte Sound	41	0	x	x
1963					
Feb. 2	Cape Flattery	7	6	x	x
May 23	Cape Flattery	6	15	x	x

[1] Serum collected day of capture; fish eviscerated and iced at this time and kidney fragments collected in port 4 days later.

AGE DETERMINATIONS

Age determinations in both halibut and English sole were made from otoliths. Personnel of the International Pacific Halibut Commission made age determinations of the halibut. English sole otoliths were treated in papain as described by Pruter and Alverson (1962) and read by the senior author.

COMPARISONS OF HM CONCENTRATION IN SERUM AND KIDNEY FLUIDS

The need to use kidney tissue to obtain qualitative data on the HM factor in English sole required us to compare concentrations of the HM factor in kidney-tissue fluids and blood serum of the same individuals.

[4] Trade names referred to in this publication do not imply endorsement of commercial products.

Table 3 makes such a comparison in 10 females taken a few weeks preceding the spawning season. An end-point fluctuation of plus or minus one serial dilution can be anticipated as part of the experimental error inherent in the technique (Kabat and Mayer, 1961). Only one fish exceeded this range.

TABLE 3.—*Comparative titers of HM factor in kidney-tissue fluid and serum of 10 English sole*

Fish number	Kidney fluid titer*	Serum titer*
1	32	64
2	32	64
3	64	64
4	64	64
5	64	128
6	32	32
7	32	32
8	64	32
9	32	128
10	32	32

*Reciprocal of last positive dilution.

In 19 female halibut, where kidney fluid and serum samples were obtained from freshly caught individuals, identical qualitative results were observed for every fish. In the halibut sample taken during June 1962, kidney fragments were obtained from carcasses that had been eviscerated and iced for 4 days, but serum samples were obtained from the same fish when freshly taken. Qualitative tests were made with both serum and kidney fluids. Quantitative tests were made with those sera which gave positive double-diffusion reactions (table 4). The only disagreements between the qualitative data for the kidney-tissue fluids and serum were the three individuals with the lowest serum concentration. The 4-day icing of the cleaned halibut carcass doubtlessly diluted the HM concentration in the adhering kidney fragments; it seems likely all tests would have agreed if the kidney tissue had been fresh.

TABLE 4.—*Comparison of HM titer of blood serum in halibut with double-diffusion reaction of kidney-fragment fluids collected from the same individuals 3 to 4 days after evisceration and icing*

Fish	Serum titer*	Kidney fluid reaction	
		Positive	Negative
Number		*Number*	*Number*
6	256	6	0
7	128	7	0
4	64	4	0
1	32	1	0
2	16	2	0
1	8	0	1
1	4	0	1
1	2	0	1
18	No reaction	0	18

*Reciprocal of last positive dilution.

The above evidence indicates that serum and freshly taken kidney-tissue fluids can be used interchangeably with considerable confidence for detection of the HM factor in these two species when qualitative data are desired.

ANALYSIS OF DATA ON ENGLISH SOLE

The six stages used by Hagerman (1952) to describe development of the ovary in the Dover sole were modified in the following manner to describe the development in the English sole:

Immature:

A. Ovaries very small (generally less than 1 g.), white, transparent, and somewhat gelatinous.

Mature:

B. Developing. Ovaries enlarging, becoming yellowish and opaque. Developing egg visible macroscopically.

C. Gravid. Ovaries very full of yellowish granular eggs.

D. Spawning. Ovaries full of transluscent eggs which run under slight pressure.

E. Spent. Ovaries flaccid; ovarian membrane vascular and sac-like.

F. Resting. Ovaries firm, white, transluscent, and somewhat gelatinous. Distinguished from stage A by the greater size.

The scale was not universally applied in this study owing to the overlap among the various stages. Stages A and F, in particular, were often difficult to distinguish; however, in November through February, including the peak of spawning in December and January (Holland, 1954; Harry, 1959), the stage A ovaries were distinct because stage F ovaries were lacking. All individuals taken during this period with ovaries in stages B through E were HM positive.

Certain individuals with stage A ovaries surprisingly were HM positive during the spawning season (table 5). Maturity classifications were made on these gonads, which were fixed in formalin. When state of maturity is not listed, the ovaries had been sectioned for histological examination before any external maturity classification was attempted. The two individuals with mature gonads had ovaries in

stages B and C, and all gonads classified as immature represented stage A. The HM-positive individuals with stage A gonads from the November samples might have matured later in the spawning season. It is unlikely, however, that the two HM-positive fish with immature gonads from the February sample would have spawned during that season, since all ovaries collected subsequently, through the July sample, were immature or spawned out.

Preliminary results of histological studies being carried out on English sole gonads by Kathleen Ladue, of our staff, were available for the lower two fish from the February sample listed in table 5. Although both were HM positive, only the ovary of the last individual showed atretic follicles as evidence of having spawned; the ovary of the other gave no histological evidence of maturing ova. This evidence supports the previous implications that the HM factor occurs in certain female English sole during the spawning season or seasons preceding that in which they are destined to spawn initially.

TABLE 5.—*HM-positive female English sole from November, December, and February samples that had gonads weighing less than 1 g., Port Orchard, Wash.*

Month of capture and maturity classification	Gonad weight	Standard body length	Age group
1963	*Gm.*	*Mm.*	
November			
Immature	0.2	207	III
Immature	.5	208	III
Immature	.5	225	III
Mature	.7	249	II
Immature	.7	250	III
Immature	.7	257	III
Immature	.9	265	III
1962			
December			
	.8	254	III
Mature	.9	245	II
1963			
February			
Immature	.5	247	II
Immature	.6	235	II
	.8	268	II
	.8	254	II
	.8	265	III

Table 6 lists the frequency of the HM factor in the various samples by age. The samples are grouped by age to follow the ovaries from the developing stage through the resting stage. Samples taken after the height of the spawning season (December and January) through July are assigned to the age they had during the spawning season, because up to July the ovaries are progressing towards the resting stage. The October and November samples are assigned to the age that they would have had at the next spawning season, because the ovaries are maturing during these months. Thus a fish entering its fourth year of life in January would be included in age-group III if taken in July, and age-group IV if taken in October.

The HM factor occurred initially in age-group II in the fish sampled in this study. The possibility of its presence in group-I fish is not ruled out because insufficient numbers of the group were sampled.

At a given age the highest frequency of the HM factor appears in the December sample at the peak of the spawning season. Frequency generally decreases through July but increases again in October and November. The occurrence of a lower HM frequency in II- and III-group fish for the March sample than for either the June or July samples is very likely the result of the bias described under Methods and Materials regarding the collection of that sample.

TABLE 6.—*Frequency of the HM factor in the various age groups of female English sole, Port Orchard, Wash.*

Month and item	Age group				
	I	II	III	IV	V[1]
1962					
December:					
Total number of fish		5	14	8	
Number positive		4	12	8	
Percentage positive		80	86	100	
1963					
February:					
Total number of fish	1	34	3		
Number positive	0	10	1		
Percentage positive	0	29	33		
March:					
Total number of fish	9	43	8		
Number positive	0	2	1		
Percentage positive	0	5	13		
June:					
Total number of fish		25	10	3	3
Number positive		8	7	3	3
Percentage positive		32	60	100	100
July:					
Total number of fish		34	16	5	11
Number positive		4	3	1	6
Percentage positive		13	19	20	55
October:					
Total number of fish		12	37	1	5
Number positive		4	26	1	5
Percentage positive		33	60	100	100
November:					
Total number of fish		11	39	5	
Number positive		2	29	3	
Percentage positive		14	74	60	

[1] Age-group V and older.

Figure 3 is a plot of the seasonal fluctuation of the HM factor with body length. Fish 22 to 25 cm. long were combined in the December sample because the separate groups had few individuals.

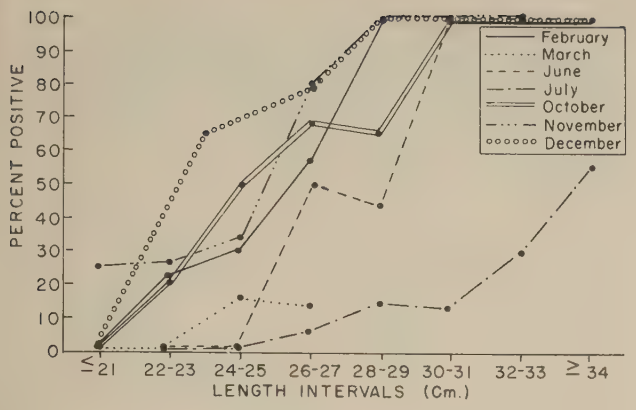

FIGURE 3.—The relation of the frequency of the HM factor to length in female English sole in different months, 1962–63, Port Orchard, Wash.

A distinct seasonal change took place between the spawning in December and the resting stage in July; during this period the HM frequency for a given length interval generally decreased. In the October and November samples, as the ovaries developed for the next spawning season, the HM frequencies in the various length intervals again increased.

Figure 3 does not take into account any growth between the December sample and subsequent collections. If seasonal growth increments were considered, most individuals 26 to 29 cm. long in December would be 30 to 33 cm. long in July. This statement is based on the assumption that El Sayed's (1959) growth estimates for English sole from Holmes Harbor in Northern Puget Sound are applicable to the Port Orchard population. A comparison of the

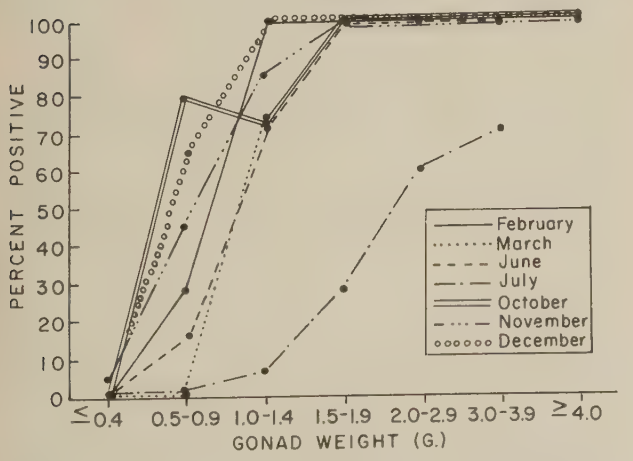

FIGURE 4.—The relation of HM frequency to gonad weights in female English sole, 1962–63, Port Orchard, Wash.

HM frequency in these two length intervals in December with the next higher interval in July still indicates a striking variation of frequency.

Ovarian weight and HM frequency are related (fig. 4). Gonad weight and HM frequency increased simultaneously. A qualitative seasonal variation in the factor's presence is again indicated. All ovaries weighing more than 1 g. that were taken during or immediately following the spawning season were from HM-positive individuals. Even a considerable number of the largest ovaries taken during the resting stage were from HM-negative individuals; HM frequency decreased as the ovarian mass decreased.

The relation between gono-somatic ratio (gonad weight expressed as percentage body weight) and HM frequency is generaly similar to that between gonad weight alone and HM frequency (fig. 5).

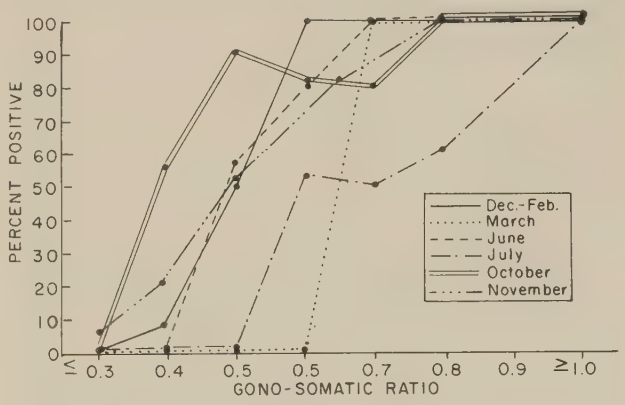

FIGURE 5.—The relation of HM frequency to gono-somatic ratios in female English sole.

The gonad weight shows the relation more clearly than the gono-somatic ratio, however, suggesting that the qualitative seasonal variations of the HM frequency are dependent more on the absolute weight of the gonad than on its mass relative to body weight.

ANALYSIS OF DATA ON HALIBUT

The HM frequency of the various halibut samples is given according to length in table 7. Fish of various ages were combined in the length intervals because of the small samples. The criterion for maturity of halibut ovaries was the presence of macroscopic ova. Personnel of the International Pacific Halibut Commission made all maturity estimates. The HM factor was detected in the serum from all female halibut that were estimated to be mature.

In the sample of June 5, 1962, which gave the best representation of different ages within a given length interval, no indication of an age dependency was detectable. In spite of the small sample sizes, the frequency of the HM factor seems to increase in length in all samples but that of February 23, 1963. This exceptional situation is discussed below.

TABLE 7.—*HM frequencies in female halibut according to length*

Date of collection	Length (cm.)							
	<85		85-100		101-110		>110	
	HM+	HM−	HM+	HM−	HM+	HM−	HM+	HM−
	Number of fish	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*	*Number of fish*
1963								
Feb. 23	2	0	3	1	1	0	0	0
1960								
Apr. 20	0	1	1	3	0	1	7	0
1963								
Apr. 23	0	0	0	2	1	1	1	1
1962								
May 11	0	0	0	2	2	0	2	0
June 5	0	0	6	10	8	8	9	0

Note.—Sampling areas shown in table 2.

As pointed out previously, we detected the HM factor during the spawning season in the serum of certain individual English sole with immature ovaries; apparently a similar condition exists in halibut. Two 76-cm. females taken in the February 23, 1963, sample at the peak of the spawning season were HM positive. [Thompson (1915) defined the spawning season for halibut as extending from December to April with the peak in February.] These fish were smaller than the minimum length reported by Thompson for mature females captured from areas included in this study, and the small ovaries did not give external indications of development. The records of serum titers of the HM-positive females in the sample of February 23, 1963, show that the two HM-positive females which were judged immature had very low titers whereas the mature individuals had titers exceeding a serum dilution of 1/250 (table 8). These findings suggest that a quantitative means may be used to distinguish maturing and mature females from immature females in which the HM factor may also be present.

In the discussion of table 4 in a preceding section, serum titers were compared with qualitative reactions of kidney-tissue fluids from the halibut sample taken on June 6, 1962. The only failures of parallel reactions were in individuals having serum dilution titers of one-eighth or less. This information indicates that kidney-fragment fluids may be useful in researchers' obtaining data relative to maturity and sex by sampling the eviscerated fish in the commercial catch upon arrival in port.

TABLE 8.—*Serum titers and maturity estimates of HM-positive females from halibut sample of February 23, 1963, taken at Cape Flattery, Wash.*

Number of fish	HM serum titer[1]	Estimate of maturity[1]
1	<2	Immature
7	<2	do
2	512	Mature
6	512	do
8	256	do
11	1,024	do

[1] Reciprocal of last positive dilution.

PRODUCTION OF HM FACTOR BY MALES

The link connecting estrogen with the production of serum components related to maturity has been determined by a number of investigators of birds, through the production of these components in males and immature females after artificial stimulation with estrogenic hormones (McDonald and Riddle, 1945; Urist and Schjeide, 1961). Bailey (1957), Urist and Schjeide (1961), and Ho and Vanstone (1961) have likewise demonstrated that artificial stimulation with estrogenic hormones produces a blood serum situation similar to that of the mature female in the teleosts *Carassius auratus*, *Paralabrax clathratus*, and *Oncorhynchus nerka*, respectively. We attempted this procedure in this study with four English sole maintained in an aquarium at the University of Washington College of Fisheries. Each fish was injected intramuscularly with 1 ml. of an aqueous suspension of estrone (5 mg./cc.). Two fish survived the initial handling (table 9). Data for the fish firmly establish the presence of the HM factor as a consequence of introducing the estrogenic hormone. Although a control bleeding was not made for fish No. 1, the rise in titer between the first and second bleeding establishes beyond doubt the effect of the estrone injection.

The HM factor was in low concentration in two male halibut taken during the spawning season. The possibility of contamination cannot be excluded because both were taken immediately following the collection of a sample from an HM-positive female, although precautions were taken to minimize contamination.

TABLE 9.—*Effect of estrone injections on the occurrence of the HM factor in the serum of male English sole*

Fish number and time of bleeding	HM reaction	Titer[1]
No. 1:		
Prior to injection	−[2]	−[2]
48 hours after injection	+	8
144 hours after injection	+	256
No. 2:		
Prior to injection	0	0
48 hours after injection	+	<8
144 hours after injection	+	256

[1] Reciprocal dilution. [2] No control bleeding.

The production of the HM factor in the serum of male English sole after estrogenic stimulations and the natural occurrence of the factor in male halibut during the spawning season indicate that males should be included in investigations of the HM factor. The natural occurrence of the factor in males may have a number of causes. Although the testes of the HM-positive male halibut appeared normal, the presence of the factor may have been due to low-level secretions of estrogenic hormones. Hermaphoditism has been reported in a diverse range of teleosts, including clupeids (Fowler, 1912), salmonids (Ross, Yasutake, and White, 1963), siluroids (Singh and Sathyaneson, 1961), cyprinodonts (Chidester, 1917), centrachids (James, 1946), and scombroids (Uchida, 1961). A further possibility is the stimulation by estrogenic hormones of exogenous origin through ingestion of mature females of smaller species of flatfish or possibly fish from other families. Estrogenic hormones are effective when administrated orally to mammals and presumably could be similarly effective in fish.

BIOLOGICAL IMPLICATIONS OF THE PRESENCE OF THE HM FACTOR

The English sole has been demonstrated to have a qualitative seasonal variation of the HM factor. The factor occurs first during the spawning season, at least as early as the second year in some individuals. After the spawning season through at least midsummer, fewer and fewer individuals retain the factor in the serum. As a new spawning season approaches, the factor gradually reappears.

Both the disappearance and the reappearance of the factor are more pronounced with increase of body length and ovarian mass. This relation may be the result of resorption of residual vitellin retained with the ovary, since the large ovaries retain a greater volume of unspawned ova.

A qualitative seasonal variation was not found in mature halibut, but we lack samples taken later than June. Thompson (1915) reported a continuous development of the ova which are to mature in the succeeding generation in the spent halibut ovary; vitellin synthesis may be a perennial process in the mature female halibut. The detection of serum vitellin in postspawning Atlantic salmon (*Salmo salar*) by Fine and Drilhon (1964) suggests its perennial occurrence in this species.

The presence of the HM factor during spawning season in immature females of both species indicates that such an occurrence may be widespread among the Pleuronectidae. Incomplete maturation preceding initial spawning in the Pleuronectidae has been reported previously. Thompson (1915) stated that contemporary investigators had found some ova in immature pleuronectid females which appeared ready to ripen but which failed to do so because the ovary, as a whole, was not yet ready. Franz (1910) reported finding this condition most marked in plaice during the last winter preceding initial spawning.

PRACTICAL APPLICATIONS OF THE HM FACTOR

As a practical procedure, the determination of the HM factor appears to have its greatest potential value in the larger pleuronectid species. In large species such as halibut or starry flounder, the sex cannot be determined at sight, except in ripe individuals. Small samples of blood taken at the time of tagging could yield information on sex and maturity without endangering the fish. Repeated bleedings of four starry flounders kept in captivity did not appear to endanger these fish. Routine practical applications to smaller species seem less likely. The sexes of smaller flatfish species, such as English sole, are generally evident by external examination; and bleeding English sole, where required in this study, caused high mortality. Evisceration of the commercial halibut catch at sea does not preclude practical application, since analysis of kidney-fragment fluids can be made after the catch arrives in port. On the other hand, smaller species are brought to port in the round and sex information can be obtained directly. Smaller species, however, are frequently more readily available in greater

numbers; they are valuable for clarification of general principles which may be applied to other species as well.

SEPARATION OF MATURE FEMALES FROM OTHER HM-POSITIVE INDIVIDUALS

Separation of HM-positive males and immature females from mature females appears possible by quantitative means. The HM serum levels of mature female halibut taken during the spawning season had titers above 200, whereas the titers of HM-positive males and immature females, which were found only at this time, were less than 2.

An extension of the single diffusion quantitation, as used in this study, may be applied where routine quantitation is required. From figure 2 it can be observed that the diameter of the precipitin ring decreases regularly as the HM concentration decreases. A measurement of the diameter of the precipitin ring formed by the undiluted fish serum could give the approximate titer.

AREAS FOR FURTHER INVESTIGATION

Several areas for further study are evident. More frequent and larger samples are desirable. As indicated above, routine quantitation may be necessary during the spawning season, and a knowledge of the quantitative seasonal fluctuation of the HM factor in a given species would be useful. Perhaps the relative HM concentration can be related to such factors as age, weight, or fecundity. More extensive histological examinations of the ovary would help, and a similar examination of the pituitary gland may establish more fundamental criteria for the occurrence of the factor. A biochemical assay might indicate that the composition of the factor in fishes is related to analogous components in other vertebrates.

THE BROADENING APPLICATION OF SEROLOGY IN FISHERY RESEARCH

Serological techniques have had increasing application in fishery problems during recent years. This research has been directed mainly toward racial studies of serum antigens or red blood cell antigens. Many of the current approaches to serological investigations of populations were discussed in a symposium moderated by Cushing (1962), and the subject has been reviewed recently by Marr and Sprague (1963) and Cushing (1964).

Antigenic differences at species level have also been investigated. Ridgway and Klontz (unpublished data) and Sindermann (1962) have found distinct species-specific antigenic characteristics in red blood cells and serum of species of Pacific salmon and Atlantic clupeiods, respectively. Ridgway (1963) reported species-specific antigens in muscle tissue of certain tuna species, in addition to species-specific blood serum components. This finding offers a possible serological means of distinguishing larvae of these species.

We hope that this study will help broaden the interest in application of serological methods to other areas of fishery biology. Because components similar to the HM factor have been detected in a diverse range of teleosts, a similar approach presumably could be used throughout this class of vertebrates. We feel that this approach can be a valuable supplement to investigating maturity in fish, though perhaps not universally applicable.

SUMMARY

A serological investigation of a serum vitellin factor in mature and maturing female flatfish was made on English sole and Pacific halibut. Immunodiffusion techniques with antisera prepared in rabbits stimulated with egg vitellin extracted from starry flounder eggs were used to detect the factor. In English sole the factor's occurrence was compared with age, length, gonad weight, and gono-somatic ratio. A qualitative seasonal variation was found; individuals with heavier ovaries during the summer were more likely to retain the factor in the serum. The presence of the factor in female halibut was compared with length, age, and maturity. A qualitative seasonal variation in mature halibut could not be studied because no samples were available during the summer or autumn. The factor was found in some immature females of both species during their spawning seasons. Production of the factor in male English sole by injections of estrogenic hormones associates synthesis of the factor in females with production of estrogen. Determination of the factor appears to have potential value as a supplement to other means of investigating maturity, particularly in large species.

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EFFECT OF WATER VELOCITY ON PASSAGE OF SALMONIDS IN A TRANSPORTATION CHANNEL

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ABSTRACT

Passage times of fish at velocities of 1 and 2 feet per second were compared in a 4-foot wide transportation channel, with a water depth of 6 feet. The timing zone was about 100 feet long.

Passage times did not differ significantly between water velocities for any one of three species: chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Salmo gairdneri*), and sockeye salmon (*Oncorhynchus nerka*). The two salmon species moved faster than steelhead trout at both water velocities.

Transportation channels for migrating adult fish are part of the fish-passage facilities at many dams. These channels vary somewhat physically, but all have the primary purpose of providing a passage area leading either to or from the fish ladders or other passage facilities. Most of the large dams on the Columbia River—Bonneville, McNary, and The Dalles, for example—have a multiple-entrance collection channel on the downstream side of the powerhouse which also serves as a transportation channel. In addition, independent channels are occasionally provided at some dams to pass fish from a single major entrance to a distant fishway. The Dalles Dam is equipped with both types (U.S. Army Corps of Engineers, 1957). These channels make it possible for one fishway to serve two or more collection points. Some channels are nearly a quarter mile long and may require up to 1,000 cubic feet per second (c.f.s.) of water for operation.

Water velocity in a transportation channel is important from the standpoint of fish passage as well as water use. Clay (1961) reported that the accepted standard velocity for ensuring continuous migration of fish through open channels is near 2 feet per second (f.p.s.). Preliminary experiments at the Fisheries-Engineering Research Laboratory at Bonneville Dam indicated that a velocity considerably less than 2 f.p.s. might be satisfactory for passage of salmonids. If so, velocity standards for transportation channels could be lowered and less water used without impeding the passage of migrating fish.

The purpose of this study [1] was to determine if salmonids would move up a transportation channel as rapidly in a water velocity of 1 f.p.s. as in 2 f.p.s.

EXPERIMENTAL EQUIPMENT

The study was made in the Fisheries-Engineering Research Laboratory at Bonneville Dam on the Columbia River. Details of the laboratory were described by Collins and Elling (1960). The experimental transportation channel (fig. 1) was 4 feet wide, 91 feet long, and operated at a water depth of 6 feet. Fish were timed over a distance of about 100 feet. (This included a short introductory area extending from a release compartment to the channel.) Water velocity was controlled by regulating the head on a weir located between the flow-introduction pool and the test channel. Headwater elevations producing velocities of 1 and 2 f.p.s. were determined before the experiment was started.

Note—Approved for publication March 8, 1966.

[1] Research financed by the U.S. Army Corps of Engineers as part of a broad program to provide design criteria for more economical and efficient fish-passage facilities at Corps projects on the Columbia River.

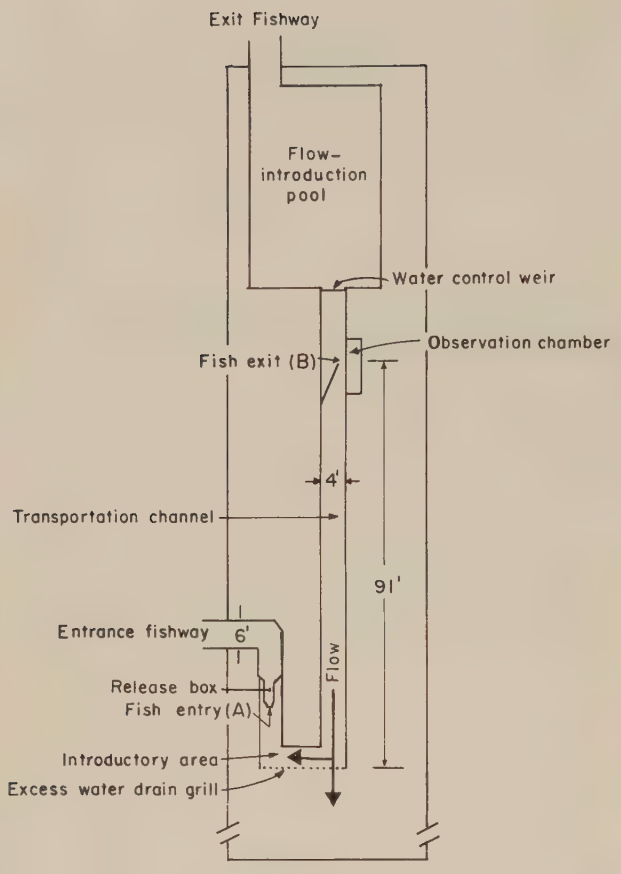

FIGURE 1.—Diagrammatic plan view of laboratory showing transportation channel and timing zone (A to B).

Velocities were measured with a cup-type current meter.

The channel was lighted by 1,000-watt mercury-vapor lights placed 6 feet apart and suspended 6 feet above the water. Light readings at the surface averaged about 700 foot-candles, which approximates light intensity on a bright cloudy day.

PROCEDURE

Salmonids used in these tests were diverted from the Washington shore fishway at Bonneville Dam. They ascended a short entrance fishway to the laboratory. Varying numbers of fish were used in each test, depending on seasonal abundance of the different species. Each fish entering the laboratory was tested only once. After a fish had completed passage through the test facility, it left the laboratory through a small exit fishway and entered the main fishway about 200 feet upstream from the laboratory.

Fish of all sizes were used; however, on a few occasions, fish were rejected because of severe cuts or other obvious physical injuries. No distinction was made as to sex.

EXPERIMENTAL DESIGN

A 2 by 2 Latin Square design used in these tests allowed 4 days (2 days at each velocity) for each test. The experiment consisted of four separate tests—two with chinook salmon (*Oncorhynchus tshawytscha*) and one each with steelhead trout (*Salmo gairdneri*) and sockeye salmon (*Oncorhynchus nerka*).

TIMING FISH

Fish entered a release compartment (fig. 2),

FIGURE 2.—Release compartment. Operator has raised gate (foreground) to allow fish to enter test area.

where they were identified as to species and released individually into the test area. Only one fish was permitted in the channel at any one time.

The timing zone (A to B, fig. 1) extended from the release compartment (A) to the exit area (B) at the upper end of the channel. A deflecting grillwork (fig. 3) directed fish toward an observation

FIGURE 3.—Exit area of test channel viewed from above. Grill on left foreground deflects fish toward viewing area (arrow) of submerged observation chamber. Flow is toward foreground.

window at the point of exit. This arrangement ensured accurate observation and timing of the fish when visibility was limited owing to turbid water. The time of entry and exit for each fish was registered on a special time-event recorder. If a fish had not completed passage of the channel within 45 minutes after time of entry, it was removed and another fish was introduced.

ANALYSIS OF PASSAGE TIME

The effect of water velocity on fish passage was determined by measuring the time required for the fish to pass through the channel. Ninety-five percent confidence intervals about the median (Dixon and Massey, 1957) were applied to test for significance of differences between passage times at the two velocities. As used here, the median is the passage time of the median fish of all fish tested in each group, including those fish that failed to complete passage within the arbitrary 45-minute time limit. Computations of the mean passage time include only those fish that completed passage of the test channel within 45 minutes.

PASSAGE TIME IN RELATION TO WATER VELOCITY

Comparisons of time required to pass through the test channel at the two velocities are given by species in the following subsections.

CHINOOK SALMON

Tests with chinook salmon were made during two periods—May 8–11 and June 12–15, 1962. Fish in the early period are normally called spring-run and those in the latter period, summer-run chinook salmon. Median passage times in the May test at water velocities of 1 and 2 f.p.s. were 3.4 and 3.9 minutes, respectively (table 1). Results of the June test were similar. Median passage times in the two velocities did not differ significantly between velocities or between tests. Mean passage times, given for comparison, suggest similar trends. In both tests, however, chinook salmon took slightly more time to pass through the channel at 2 f.p.s. than at 1 f.p.s. (fig. 4). This difference corresponds with observations by Weaver (1963), who found that chinook salmon moved more slowly as velocity increased in the range of 2 to 8 f.p.s.

TABLE 1.—*Median and mean passage times of chinook salmon in an experimental transportation channel at Bonneville Dam at water velocities of 1 and 2 f.p.s., May and June 1962*

Test period	Water velocity	Fish tested	Passage time			
			Median	Lower limit[1]	Upper limit[1]	Mean
	F.p.s.	*Number*	*Minutes*	*Minutes*	*Minutes*	*Minutes*
May 8–11	1	37	3.4	2.7	5.5	4.7
	2	44	3.9	3.2	4.5	[2]4.9
June 12–15	1	45	3.1	2.5	4.4	4.8
	2	75	3.6	2.7	4.2	5.3

[1] 95-percent confidence intervals about the median.

[2] One fish failed to complete passage within the 45-minute time limit and was not included in computation of the mean.

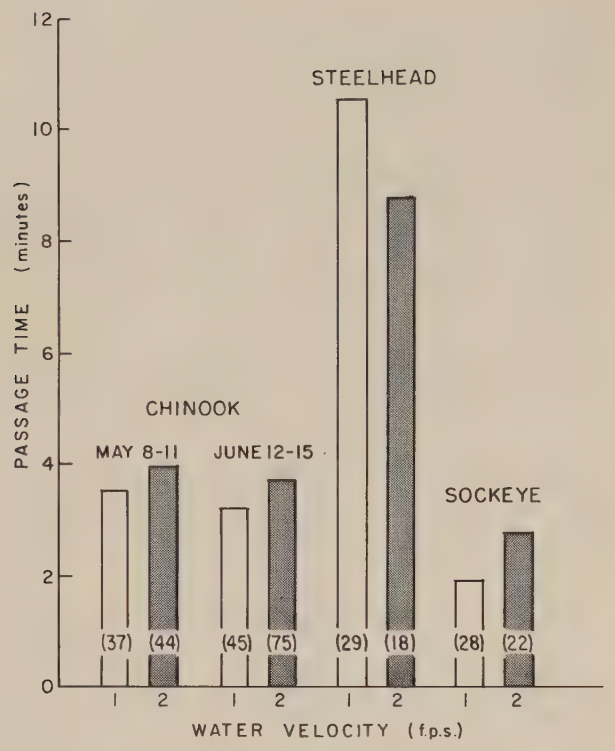

FIGURE 4.—Median passage times of chinook salmon, steelhead trout, and sockeye salmon in a transportation channel at water velocities of 1 and 2 f.p.s., 1962. Numbers of fish tested are shown in parentheses near the base of each bar.

STEELHEAD TROUT

Median passage times of steelhead trout at water velocities of 1 and 2 f.p.s. were 10.6 and 8.8 minutes, respectively (table 2). This difference was not statistically significant. Mean passage times were similar to the medians. Steelhead trout moved somewhat faster at the higher velocity, in contrast to the difference in chinook salmon (fig. 4). Weaver (1963) observed similar performances among steelhead trout, i.e., faster movement as water velocity increased.

In comparison with the other species tested, steelhead trout obviously spent considerable time in the test channel. Given suitable hydraulic conditions, steelhead trout frequently remain in favored pools or runs for varying periods of time before proceeding upstream. This characteristic possibly accounts for the relatively slow passage times of this species in the present tests.

SOCKEYE SALMON

Performances of sockeye salmon at the two water velocities were similar to those of chinook salmon. Both the median and mean passage times (table 3) give evidence of a slightly faster passage at the lower velocity. The difference between median passage times, however, was not significant.

TABLE 2.—*Median and mean passage times of steelhead trout in an experimental transportation channel at Bonneville Dam at water velocities of 1 and 2 f.p.s., July 30–August 2, 1962*

Water velocity	Fish tested	Passage time			
		Median	Lower limit[1]	Upper limit[1]	Mean
F.p.s.	*Number*	*Minutes*	*Minutes*	*Minutes*	*Minutes*
1	29	10.6	5.4	15.0	[2]9.6
2	19	8.8	3.0	11.0	[3]8.1

[1] 95-percent confidence intervals about the median.
[2] Four fish failed to complete passage within the 45-minute time limit and were not included in computation of the mean.
[3] Excludes one fish that did not complete passage within 45 minutes.

TABLE 3.—*Median and mean passage times of sockeye salmon in an experimental transportation channel at Bonneville Dam at water velocities of 1 and 2 f.p.s., July 10–13, 1962*

Water velocity	Fish tested	Passage time			
		Median	Lower limit[1]	Upper limit[1]	Mean
F.p.s.	*Number*	*Minutes*	*Minutes*	*Minutes*	*Minutes*
1	28	1.9	1.5	3.3	3.1
2	22	2.7	2.0	5.7	[2]4.1

[1] 95-percent confidence intervals about the median.
[2] One fish failed to complete passage within the 45-minute time limit and was not included in computation of the mean.

CONCLUSION

A water velocity of 1 f.p.s. is as suitable as one of 2 f.p.s. for the passage of chinook salmon, steelhead trout, and sockeye salmon in a transportation channel.

ACKNOWLEDGMENTS

Gerald B. Collins and Carl H. Elling assisted in planning the experiments. William S. Davis suggested the experimental design, and the staff at the Fisheries-Engineering Research Laboratory aided in carrying out the work.

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COMPARATIVE ANATOMY AND SYSTEMATICS OF THE TUNAS, GENUS *THUNNUS* [1]

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ABSTRACT

The taxonomic status of the tunas of the world, often placed in the genera *Thunnus, Germo, Neothunnus, Parathunnus,* and *Kishinoella,* is assessed through the use of external morphological and internal anatomical characters. Seven species, all included in the single genus *Thunnus,* are considered valid: *T. thynnus,* the bluefin tuna; *T. alalunga,* the albacore; *T. obesus,* the bigeye tuna; and *T. albacares,* the yellowfin tuna, are circumglobal in distribution; *T. atlanticus,* the blackfin tuna, and *T. tonggol,* the longtail tuna, are restricted to the western Atlantic and the Indo-West Pacific, respectively; *T. maccoyii,* the southern bluefin tuna, is known in the southern Pacific and Indian oceans and off northwestern Australia. Two subspecies of *T. thynnus* are recognized: *T. t. thynnus* in the Atlantic and *T. t. orientalis* in the Pacific.

In Part 1 the comparative anatomy is described and characters are given for differentiating the species by means of counts and measurements and by comparison of the skeletal, visceral, and vascular systems. In Part 2 the genus *Thunnus* is characterized with respect to other genera of Scombridae, and for each species a synonymy, a résumé of distinctive characters, discussion of type specimens and nomenclatural problems, and a review of known geographic distribution are given.

The purpose of this paper is to demonstrate that there are, at most, seven species of tunas in the world, and that they should be placed in the single genus *Thunnus* which is circumglobal in distribution and constitutes one of the most important groups of commercial fishes. Much time and money have been expended in gathering meristic, morphometric, anatomical, distributional, and life-history data, yet the systematic and nomenclatural status of the group remains unsatisfactory. Over the years, 10 generic names and 37 specific names have been applied to the seven species which we recognize. The confusion is due, at least in part, to the pelagic habits of all of the species and to their large adult size, which makes specimens difficult to preserve and store and requires that observations be made at the time of collection, often under adverse conditions. Study material over the great size range is not easily obtained, so that growth changes are hard to evaluate. The economic importance of the group has led many biologists to dabble in tuna taxonomy, using variable characters and different means of counting and measuring. Provincialism has caused otherwise competent workers to believe that the kinds of tunas in their home areas are unique and to cling tenaciously to locally established names despite contrary evidence.

Our studies have been built upon the work of a number of previous investigators. We have come to realize, as many of these workers have, the great value of internal anatomical characters as a means of distinguishing tuna species. In this field, Kishinouye (1915, 1917, 1923) pioneered. The most extensive

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and painstaking anatomical descriptions are found in his works and those of Godsil and Byers (1944) and Godsil and Holmberg (1950).

This paper is divided into two major sections. The first part describes and compares the osteology, viscera, vascular system, meristic characters, morphometry, and coloration among the species. The second part considers the systematic position of the genus *Thunnus*. Each species is treated separately, including a synonymy, diagnosis (based on characters from the first section), discussion of nominal species, and outline of geographical distribution.

MATERIALS AND ACKNOWLEDGMENTS

We have examined, measured, and made counts on numerous specimens of all Western Atlantic species. Many specimens taken in pound nets in Cape Cod Bay were made available through the courtesy of John E. Vetorino, Mike Goulart, and Adam Rupkus. Most material for dissection and a large share of the total specimens examined were collected on exploratory longline cruises, by the Bureau of Commercial Fisheries vessels *Delaware* in the Gulf Stream and adjacent waters east to the Azores and *Oregon* in the Gulf of Mexico and Caribbean Sea. For saving valuable specimens and for allowing us to participate in many cruises, we are particularly indebted to Harvey R. Bullis, Peter C. Wilson, and James L. Squire. The late Al Pflueger of Miami, Fla., and Frank J. Mather III of Woods Hole Oceanographic Institution (WHOI), gave us a number of specimens. Edward C. Raney lent us skeletons from Cornell University. Margaret E. Watson of WHOI and Donald P. de Sylva of the University of Miami Institute of Marine Science allowed us to examine other specimens.

Southeast Pacific specimens of *T. obesus* and *T. albacares* were dissected during our participation in cruise 14 of the *Anton Bruun*, part of the South East Pacific Biological Oceanographic Program sponsored by the National Science Foundation. Australian and Japanese tunas were examined in the fish markets of Tokyo and Yaizu. We obtained whole specimens or skeletal material of Pacific species from the Inter-American Tropical Tuna Commission (M. B. Schaefer and Craig Orange); California State Fisheries Laboratory (Phil Roedel and Harold B. Clemens); Bureau of Commercial Fisheries Biological Laboratory, Honolulu (John C. Marr); Nankai Regional Fisheries Laboratory, Kochi, Japan (Hiroshi Nakamura and Shoji Ueyanagi); Tokyo University (Tokiharu Abe); Kyoto University, Maizuru, Japan (Izumi Nakamura and Tamotsu Iwai); Institut Français d'Océanie, Noumea, New Caledonia (Michel Legand); and C.S.I.R.O. Marine Laboratory, Cronulla, Australia (J. C. Moore and J. P. Robins).

Specimens from the Indian Ocean were received from the Nankai Laboratory and from cruises of the *Anton Bruun* made during the U.S. Program in Biology of the International Indian Ocean Expedition. Frank H. Talbot and Michael Penrith provided South African specimens and skeletons.

We examined specimens and skeletons of both Atlantic and Pacific forms at the California Academy of Sciences (W. I. Follett); Stanford University (George S. Myers and Warren C. Freihofer); University of California at Los Angeles (Wayne J. Baldwin); Scripps Institution of Oceanography (Richard H. Rosenblatt); and the U.S. National Museum and skeletons of Pacific and Indian Ocean specimens at Kyoto University, Maizuru (Tamotsu Iwai and Izumi Nakamura) and the Nankai laboratory (Shoji Ueyanagi).

All available types were examined at the Muséum National d'Histoire Naturelle (MNHN), Paris (M. L. Bauchot and C. Roux); at the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden (M. Boeseman); and at the Academy of Natural Sciences, Philadelphia (ANSP) (James E. Böhlke). We received information on types in the Australian Museum in Sydney and the Dominion Museum in Wellington from Frank H. Talbot and J. Moreland, respectively.

We made thorough examinations of viscera and blood vessels on the following (sizes in mm.):

Thunnus alalunga 9 Atlantic (780–1,250), 1 Pacific (992), 2 Indian (ca. 900–970)
Thunnus albacares 15 Atlantic (600–1,515), 4 Pacific (670–941), 11 Indian (601–895)
Thunnus atlanticus 21 (322–665)
Thunnus obesus 17 Atlantic (697–1,545), 5 Pacific (851–1,614), 2 Indian (630–680)
Thunnus maccoyii 3 (742–1,442)
Thunnus thynnus thynnus 10 (316–2,315)
Thunnus thynnus orientalis 3 (614–1,450)
Thunnus tonggol 4 (373–924)

The following complete skeletons (most of which are now in the U.S. National Museum) provide the basis for our analysis. These include a large share of the material of Godsil and Byers (1944) and Godsil

and Holmberg (1950). Range of skull lengths, in mm., in parentheses.

Thunnus alalunga 19 Atlantic (125–167), 26 Pacific (99–152), 2 Indian (146–157)
Thunnus albacares 21 Atlantic (98–196), 26 Pacific (49–149), 12 Indian (101–127)
Thunnus atlanticus 26 (51–111)
Thunnus obesus 21 Atlantic (119–215), 5 Pacific (97–237), 4 Indian (112–178)
Thunnus maccoyii 9 Australia (111–219), 4 South Africa (128–218), 4 SE. Pacific (207–238)
Thunnus thynnus thynnus 21 Atlantic (76–335), 1 South Africa (322)
Thunnus thynnus orientalis 40 (34–294), 1 SE. Pacific (290)
Thunnus tonggol 2 East Australia (122–128), 6 Indian (56–99).

Details were corroborated by numerous partial dissections of all species. We also examined many additional skulls, postcranial skeletons, and radiographs.

We are grateful to Daniel M. Cohen, J. A. F. Garrick, Brian J. Rothschild, Donald W. Strasburg, Frank H. Talbot, and Stanley H. Weitzman for making comments on various drafts of the manuscript. Mildred H. Carrington and Gale G. Pasley made most of the figures from our sketches. Alice Holland typed many drafts of the manuscript. John E. Fitch made it possible to use the plate blocks from Godsil and Byers (1944) for figures 20 and 21.

METHODS

Dissections.—Although numerous partial dissections of both preserved and fresh specimens were made, the most thorough work was done with fresh specimens on shipboard or, more often, with frozen specimens in the laboratory. After the fish thawed, colored latex was injected into the arteries and veins through the lateral cutaneous branches that had been exposed by removing the thick skin behind the pectoral fin base. Often the injection mass did not reach the posterior ends of the cutaneous vessels or the posterior commissure, but these vessels ordinarily could be followed rather easily. In the other direction, the injection mass seldom penetrated beyond the liver, partly because the deeper regions were not completely thawed. After the latex had set, the lateral cutaneous system was studied. The ventral wall of the body cavity was then removed and the viscera drawn in situ. The ventral organs were then turned aside or removed to expose the swimbladder, and this, in turn, was removed and the dorsal fibrous connective tissue cut to expose the kidney and ureters. The most difficult aspect of the dissection involved exposing and tracing the anterior arteries, which lie so far forward and are so deep that they are difficult to reach without mutilating the branchial region. After the appropriate observations were completed, the specimen was fleshed and the skeleton cleaned.

Counts and measurements.—Most external counts and measurements were made on fresh or frozen specimens, some on preserved material, according to the methods described by Marr and Schaefer (1949), with the following exceptions. Our fork length is what they called "total length." We measured length of bony orbit rather than diameter of iris; in our comparisons, therefore, we used only our own data for this character. (We do not recommend this procedure for future workers.) We did not measure "pectoral insertion to insertion first dorsal," or "length longest dorsal finlet," but we made the following measurements not mentioned by Marr and Schaefer: Snout to insertion of pectoral fin, maximum width of body, pelvic fin length, insertion of pelvic fin to vent, tip of depressed pelvic fin to vent (all of which are self-explanatory), snout length (snout tip to front edge of bony orbit), and interorbital width (least distance between dorsal rims of bony orbits formed by frontal bones).

Measurements made by the same worker of the same specimen before and after freezing may differ enough to negate a morphometric difference between species, therefore, all morphometric characters should be used only with rather wide margins for error.

Skeletons.—Skull length was measured from the anterior tip of the vomer to the lower posterior end of the ankylosed first vertebral centrum. Individual bones of the skull, pectoral girdle, and pelvic girdle were compared simultaneously in all species, and measurements were made only when proportional differences were suspected. The only significant differences requiring measurements for definition were among those already pointed out by Godsil and Byers (1944) or Godsil and Holmberg (1950). Dial calipers were used in most cases, and articulation cartilages were removed from skull bones. The methods of mensuration follow.

Anterior articulating head of hyomandibula (See fig. 6). Length (B) was measured from the end of the horizontal articulation surface (pterotic head) to the most anterior point of the anterior articulation

surface (sphenotic head). Least width (A) and greatest width were measured vertically on the anterior (sphenotic) head.

Metapterygoid (See fig. 7). The transition from anteroventral (C) to posteroventral (D) margin is usually an arc. Each margin was measured to the midpoint of the arc.

Quadrate (See fig. 8). Length (G) was measured from the most ventral part of the articular condyle to the tip of the spine. Width of horizontal edge (F) was measured along the horizontal dorsal edge to the point where it forms a slight depression before the spine. Total width (E) was measured from the anterior point of the horizontal dorsal edge along a projection of the line of this edge to the posterior margin of the spine.

36th vertebra. Length was measured along the axis of the centrum from the outer anterior rim to the outer posterior rim. Width was measured vertically on the lateral surface at the narrowest part of the centrum and does not include the neural or haemal arches.

Bone terminology is that of de Sylva (1955), which has been used for tuna osteology by most other recent workers. A number of names differ from those accepted by many fish osteologists.

PART 1. COMPARATIVE ANATOMY

The morphological characters useful for distinguishing the species of *Thunnus* fall into seven groups: osteology, viscera, vascular system, olfactory organ, meristic characters, morphometric characters, and coloration. These will be discussed in this order in this section of the paper. The first three groups, osteology, viscera, and vascular system, include the most important characters.

OSTEOLOGY

Osteological characters are very important in distinguishing species of *Thunnus*. They have an advantage over characters in the soft anatomy in that the bones can be saved so future workers can reexamine the material on which a study is based. We have used a large amount of the material Godsil and his co-workers reported on. Four groups of osteological characters will be considered: neurocranium, branchiocranium, pectoral and pelvic girdles, and vertebral column. The most useful characters are in the skull and the vertebral column. Each of the four groups will be discussed separately, giving a general osteological description followed by an enumeration of the specific characters.

Neurocranium

General characteristics.—Details of the general neurocranial structure of tunas have been illustrated by Masterman (1894), Kishinouye (1923), Frade (1932), Gregory (1933), Godsil and Byers (1944), de Sylva (1955), and Nakamura (1965). The accompanying labeled figures of an albacore (*Thunnus alalunga*) skull show the bones of the neurocranium (figs. 1–3). Photographs of the skulls of six of the seven species of *Thunnus* are presented in appendix figs. 1–3.

The skull of a tuna, compared with that of most typical percoid fishes, is short and wide. In dorsal view (fig. 2), at its anterior end, the dermethmoid (= ethmoid) is wide and its anterior margin only slightly curved. The interorbital region is broad, and the otic region broader still. A prominent dorsolateral crest is formed on each side by the frontal, parietal, and epiotic bones; each of the epiotics bears a short, posteriorly directed process. The lateral edges of the frontal and pterotic, making up the sides of the roof of the neurocranium, form a more prominent and rather flat sharp crest on each side which extends posteriorly as a long plate-like pterotic spine. The supraoccipital crest is high and extends posteriorly over the first few vertebrae.

Ventrally, the dentigerous vomer (= prevomer) is flanked by broad processes of the parethmoids (= lateral ethmoids). Most of the base of the skull is formed by the parasphenoid, which is flat or slightly concave in its anterior two-fifths, bears a medial, ventrally directed crest in the next two-fifths, and posteriorly is first convex, then deeply concave, with dorsomesially curved lateral flanges that enclose a parasphenoid chamber. Lateral wings project dorsad from near the end of the ventral crest to form part of the posterior myodome.

In lateral view, the alisphenoids (= pterosphenoids) form a partial interorbital septum extending ventrad from the roof of the skull. In extreme cases (large *Thunnus thynnus*) this septum may be fused with the parasphenoid, to form a bony septum partially separating the orbits. In the posterior part of the

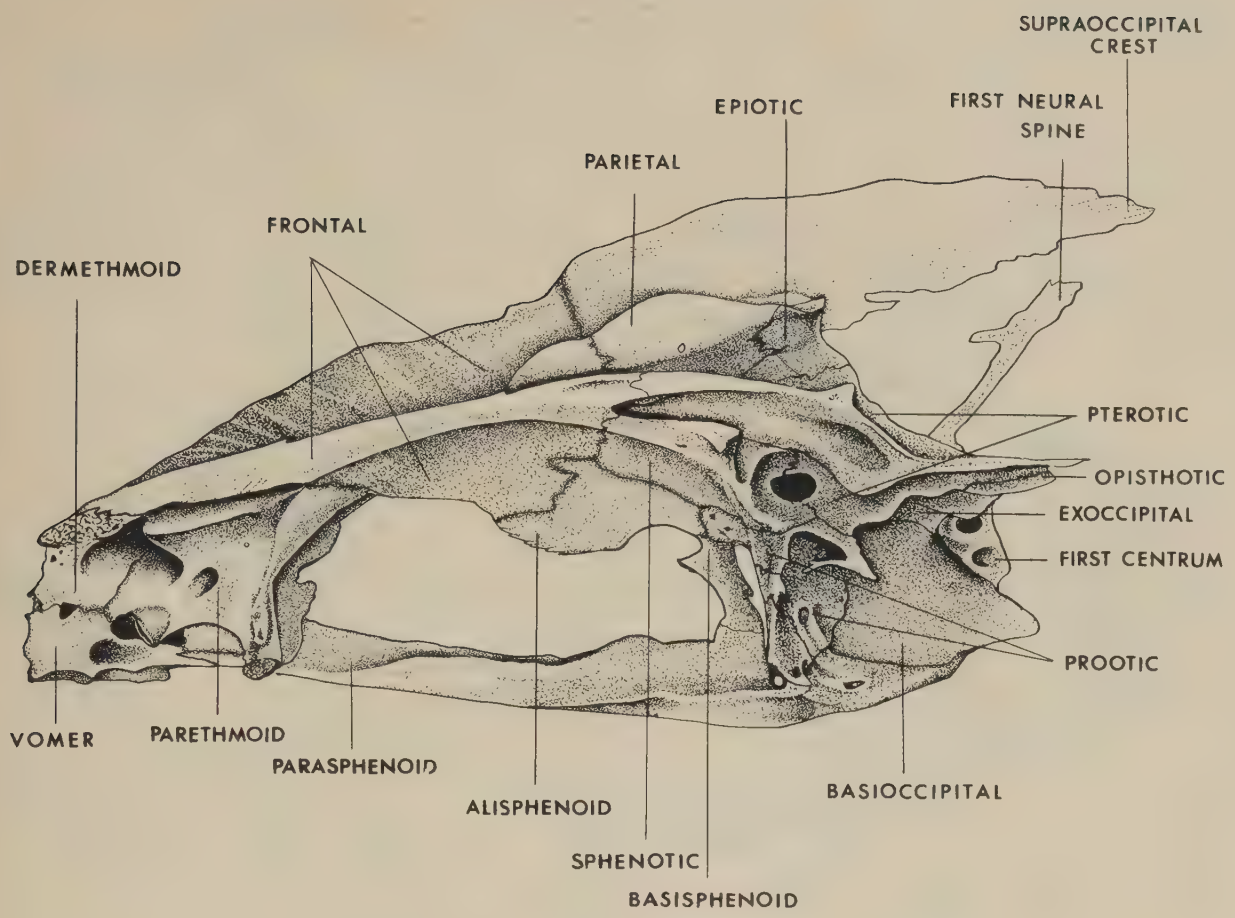


FIGURE 1.—Skull of *Thunnus alalunga*. Lateral view.

orbital region is a median, vertically oriented basisphenoid, which usually has an anteriorly directed process near its dorsal end. The posterior base of the cranium is formed by the end of the parasphenoid (ventral profile) and the lateral flanges of the basioccipital (posterior profile). The first vertebra articulates firmly, partly by a jagged suture, with the occipital region and forms an integral part of the skull. One end of Baudelot's ligament attaches to the basioccipital, the other end to the supracleithrum.

The prootic pits (Godsil, 1954) are large pouchlike concavities on each side of the ventral surface of the cranium, opening posteriorly and separating the pterotic bones from the brain case. Part of the roof, floor, and sides of each prootic pit is formed by the prootic bone, and the anterior wall by the sphenotic. The pits function as areas of attachment for the branchial musculature. These pits are characteristic of the most advanced scombrids—*Thunnus, Euthynnus, Katsuwonus, Auxis,* and *Allothunnus*—and are incipient in *Sarda* (Starks, 1910; Godsil, 1954).

The posterior myodome is a deep median depression opening anteriad at the posterior end of the orbital region. Its anterolateral walls and roof are formed by the prootics, its floor and ventrolateral walls by the parasphenoid, and its posterior concave wall by the basioccipital. The posterior myodome functions as a place of attachment for the rectus muscles of the eyes. The narrow basisphenoid lies just anterior to the anterior opening of the posterior myodome. There is a posterior or parasphenoidal chamber (Kishinouye, 1923), which communicates with the posterior myodome and is formed by the upcurved walls of the posteriormost end of the parasphenoid.

A large triangular fronto-parietal foramen (lateral parietal foramen of Masterman, 1894) is present on each side of the dorsal surface of the skull, at the junction of the frontal, parietal, and supraoccipital

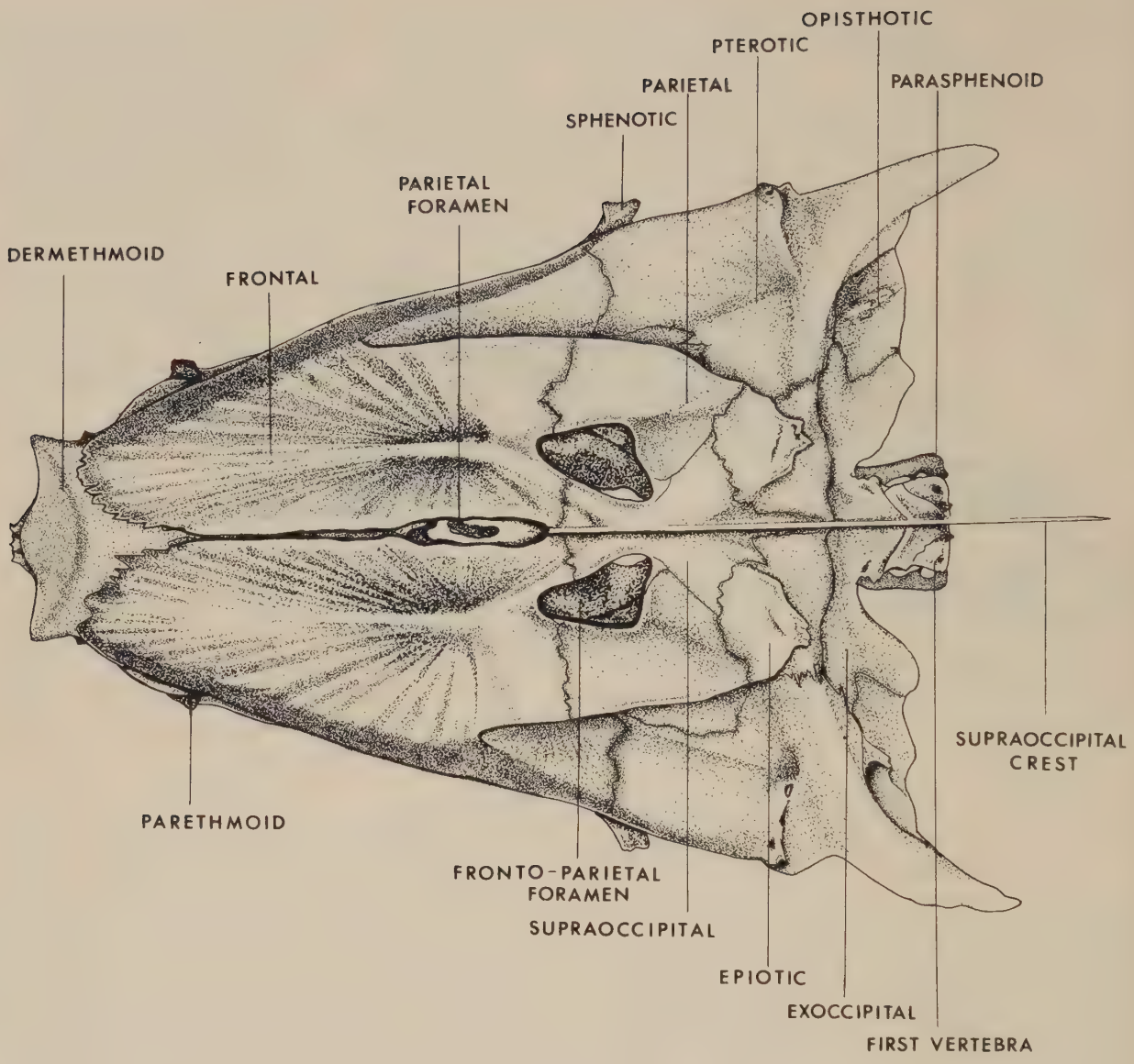


FIGURE 2.—Skull of *Thunnus alalunga*. Dorsal view. [The pineal foramen is incorrectly labeled as parietal foramen.]

bones. In life these foramina are covered by a tough membrane and are not passages for nerves or blood vessels. We were unable to determine their function. Fronto-parietal foramina are characteristic of *Thunnus*, *Euthynnus*, and *Katsuwonus*, and the bone is thin in this area in several other scombrids.

There is a prominent medial pineal foramen between the edges of the frontal bones, just anterior to the supraoccipital crest. Rivas (1954a) has suggested that in *T. thynnus* light can pass through the transparent "window" in the skin over this foramen and then down to the brain through the cartilaginous lens that fills the foramen in life. He postulated that the pineal apparatus has a phototropic function involved in migration. Holmgren (1958) also studied the pineal apparatus of *T. thynnus* but could find no evidence of a photoreceptive role for the pineal organ. The pineal foramen is characteristic of the more advanced members of the Scombridae and is absent or represented by only a small slit in the more primitive genera such as *Scomber*, *Rastrelliger*, and *Scomberomorus* (Allis, 1903; Kishinouye, 1923; Mago Leccia, 1958).

Specific Characters.—Four neurocranial characters

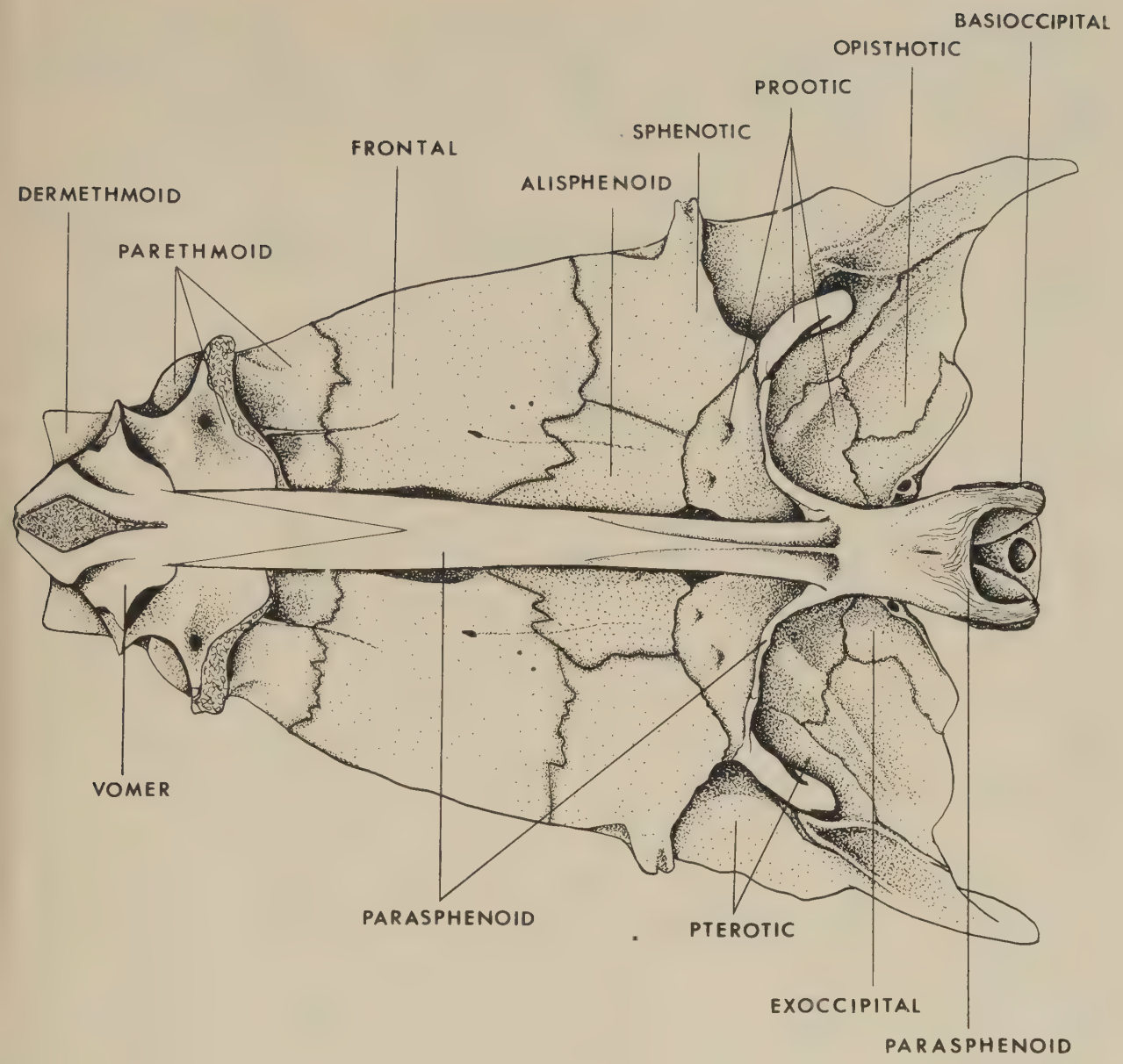


FIGURE 3.—Skull of *Thunnus alalunga*. Ventral view.

have been found useful in distinguishing the species of *Thunnus:* the alisphenoids, posterior parasphenoid margin, supraoccipital crest, and ventral parasphenoid shaft. They are characteristic of specimens from all oceans.

Alisphenoids (fig. 4). The alisphenoids meet in the median line and extend ventrad into the orbit. They approach the parasphenoid more closely in *T. thynnus* and *T. maccoyii* than in the other tunas. The greatest height of the anterior part of the orbit, B, measured from dorsal parasphenoid to upper median part of parethmoid, was divided by the least distance between alisphenoid and parasphenoid, A. In 46 skulls of *T. thynnus*, 16 have the alisphenoids fused to the parasphenoids; in the remaining 30, A goes into B 2–15 times; with a mean ($\bar{x}$) of 4.8, only in 6 specimens is the ratio less than 2.5. No fusion was observed in *T. maccoyii;* in 17 skulls the ratio was 2.0-10.3, $\bar{x}$ 4.8. By contrast, in all other species, A goes into B 1–3 times. Among 122 skulls of the other species, only 3 *T. albacares* and 2 large *T. tonggol* have a ratio of 2.5 or greater. Mean

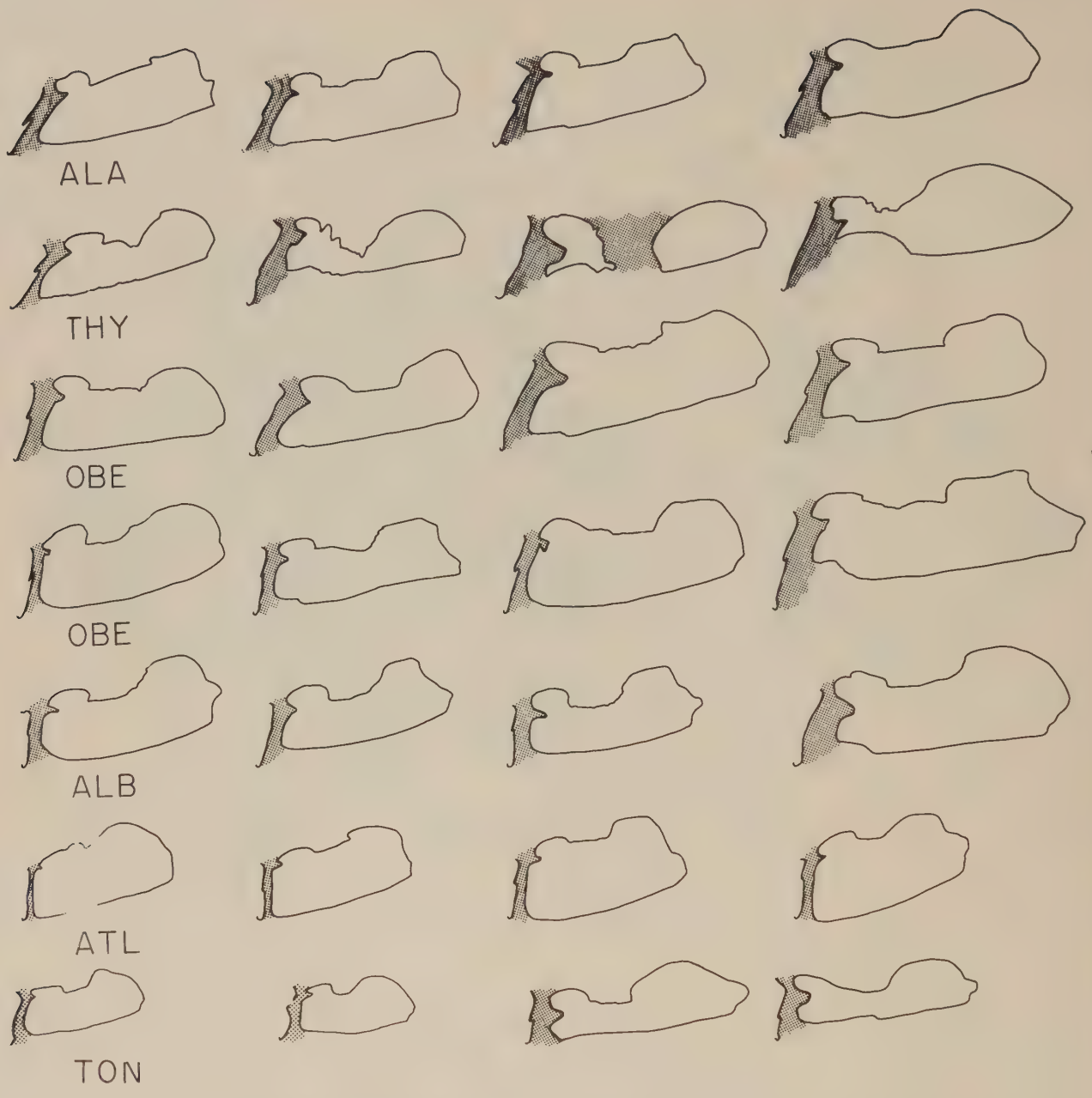


FIGURE 4.—Skulls of *Thunn* Right lateral view of orbital region of neurocranium showing conformation of basisphenoid (stippled) and a... d. Arrangement within each species in order of increasing skull lengths from left to right: ALA—*T. alalunga*, 131, 138, 150, 167 mm. ALB—*T. albacares*, 103, 116, 122, 179 mm. ATL—*T. atlanticus*, 51, 80, 97, 102 mm. OBE—*T. obesus:* upper-Atlantic, 170, 181, 185, 207 mm.; lower-Pacific, 97, 142, 147, ca. 240 mm. THY—*T. thynnus*, 76, 139, 231, ca. 320 mm. TON—*T. tonggol*, 57, 61, 122, 128 mm.

values are: *T. tonggol* ($N=8$) 2.0; *T. albacares* ($N=43$) 1.8; *T. obesus* ($N=32$) 1.6; *T. alalunga* ($N=27$) 1.6; *T. atlanticus* ($N=14$) 1.2.

Posterior parasphenoid margin (fig. 5). The portion of the parasphenoid forming the walls of the parasphenoidal chamber is partially covered laterally by the basioccipital. Together the margins of these bones extend ventrad from the first vertebra, either vertically or slanting forward or backward; anteriorly the parasphenoid alone forms the margin. With due consideration for growth changes and individual variation, the profile formed at this part of the skull

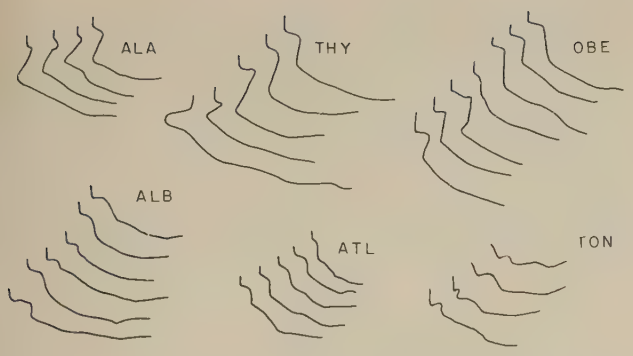


FIGURE 5.—Skulls of *Thunnus* species. Right lateral view of posteroventral part of neurocranium showing conformation of posterior parasphenoid margin. Arrangement within each species in order of increasing skull length from right to left. ALA—131, 138, 150, 167 mm. ALB—103, 107, 116, 122, 169, 179 mm. ATL—51, 80, 88, 97, 102 mm. OBE—Pacific, 97, 141, 143, 146, 165, 189, 210 mm. THY—76, 139, 230, 335 mm. TON—57, 61, 122, 127 mm.

is quite characteristic of some species.

In *T. thynnus*, *T. maccoyii*, and *T. alalunga* a decided angle is formed by the posterior parasphenoid margins. The acuity of the angle and its posterior extent generally increase with size in *T. thynnus* (fig. 5), and extreme development of the angle is found in very large specimens. Within its observed size range (skull length 88–167 mm.), *T. alalunga*, however, displays a more acute angle than does *T. thynnus* of similar size. *T. maccoyii* resembles *T. thynnus* in this respect.

In relatively large specimens of *T. obesus* the angle is apparent but not as acute as in *T. thynnus*, *T. maccoyii*, and *T. alalunga*. Observations of Pacific specimens indicate probable changes with growth. The two smaller eastern Pacific specimens reported by Godsil and Byers (1944) and again by de Sylva (1955) have rounded margins, but other eastern Pacific specimens within the same size range show a definite angle.

T. albacares, *T. atlanticus*, and *T. tonggol* exhibit great variation. Some have unmistakably rounded margins; others are somewhat angulate but have a very short distance from the first vertebral centrum to the apex of the angle, so that the angle itself is never obvious.

Supraoccipital crest. In *T. alalunga* (fig. 1) the supraoccipital crest is relatively more slender than in any of the other species of *Thunnus* and is longer, nearly always reaching at least to the centrum of the third vertebra. In the other six species the crest rarely extends beyond the second vertebra.

Ventral parasphenoid shaft. In *T. atlanticus* the anterior portion of the parasphenoid shaft is concave ventrally (de Sylva, 1955). In *T. tonggol* we found it concave in three small specimens (skull length 57–99 mm.) and flat in two larger specimens (skull length 122–128 mm.). It is most commonly flat or slightly convex in the other species, but a degree of concavity has been observed in individuals, especially young, of all except *T. obesus*.

Other characters.—Godsil and Byers (1944) cited several additional neurocranial characters that are supposedly useful in distinguishing among the species. In our estimation, none of these is valid for the following reasons.

The parietal crest in *T. albacares* was described as extending farther forward than in *T. obesus* so that a projection of the curvature of the lateral edge of the parethmoid (prefrontal of Godsil and Byers) would be continuous with the parietal crest in *T. obesus* but would run below it in *T. albacares*. Our material shows both conditions in all species.

The angle of the long axis of the basisphenoid relative to the parasphenoid is highly variable and not reliable as a specific character. The width of the basisphenoid relative to its height is not only variable within any given size range but also changes with growth.

The anteriorly directed process at the upper end of the basisphenoid was used by de Sylva as a distinguishing character (1955: 32–35). He described the process in *T. albacares* and *T. "sibi"* (Pacific *T. obesus*) as being directed obliquely ventrad so that a line drawn through its axis would transect the parasphenoid at or behind the junction with the parethmoid; in *T. thynnus*, *T. alalunga*, and *T. atlanticus* such a line would more nearly parallel the parasphenoid and would not cross it. We find this character variable within a species. Furthermore, in larger fishes, the entire bone becomes relatively shorter and wider, whereas, the process becomes broader and more rounded.

The head of the vomer in *T. alalunga* was described as having a thin bony ridge behind the dentigerous anterior portion, a similar ridge being present in some *T. thynnus*, but not in *T. albacares* or *T. obesus*. Actually, all the species may have such a ridge. In *T. alalunga* teeth are generally restricted to the anterior end; the posterior end is very thin. The other species usually, but not always, bear teeth along the entire ridge, and the posterior portion is wider. In *T. atlanticus* the ridge is usually absent.

These tendencies exist, but frequent exceptions render the character uncertain.

A depression in the dorsal profile just anterior to the supraoccipital, reported to be present in all species but most pronounced in *T. thynnus*, is related to the pineal foramen. We find this variable in all species and distinctive in none.

In the contour of the posterior margin of the sphenotic as seen in ventral view, we can detect no difference among the species. A concave curvature of the margin, held by Godsil and Byers to be characteristic of *T. alalunga* and *T. thynnus*, is not only slight but may be present or absent in all species.

Branchiocranium

General description.—The branchiocranium includes the branchial bones, opercular apparatus, jaws, and associated bones. On each side the dentigerous premaxilla forms the upper jaw, and the maxilla is located dorsomesial to it. A small supramaxilla is attached to the posterior end of each maxilla. The lower jaw includes the dentary, which bears teeth; the articular, forming the rear end of the jaw and articulating with the condylar region of the quadrate; and a small angular at the posteroventral corner of the articular. The suspensorium begins with the hyomandibula, which articulates at its upper end with the otic region of the neurocranium and with the opercle. The ventral limb of the hyomandibula articulates with the metapterygoid, and the ventral portion of the latter in turn articulates with the symplectic and quadrate. To the anteroventral part of the metapterygoid are joined the basal portions of the endopterygoid and ectopterygoid. At their anterior ends, these are joined to the short, dentigerous palatine, which articulates with the condyle of the anterior end of the maxilla.

In addition to the hyomandibula, the hyoid arch is composed of two median and four paired bones. A glossohyal supports the tongue, and a urohyal lies below and between the two sides of the arch. The paired bones include small basihyals, large ceratohyals that articulate with smaller epihyals by jagged, toothlike sutures on the mesial side only, and small interhyals posteriorly joining the operculum.

In the branchial arches are three median basibranchials (a small cartilage posterior to the third may represent a fourth basibranchial, see Iwai and Nakamura, 1964a) and on each side three hypobranchials, five ceratobranchials, four epibranchials, and four pharyngobranchials. The posteriormost ceratobranchials and mesial three pairs of pharyngobranchials bear villiform teeth. The anterior surfaces of the first four arches bear gill rakers, and, as supports for the gill filaments, so-called gill bars are found on the posterior surfaces (Iwai and Nakamura, 1964a).

Specific Characters.—Differences worthy of note have been described for only six bones by Kishinouye (1923) or Godsil and Byers (1944). These are the hyomandibula, metapterygoid, quadrate, subopercle, interopercle, and ceratohyal. We concur in their observations on the first four only.

The anterior (sphenotic) articulating head of the hyomandibula (fig. 6) is relatively longer and narrower in *T. alalunga* than in the other species. The proportion of length to least width in our specimens ranged as follows: *T. alalunga* ($N=35$) 1.7–2.7, $\bar{x}=2.2$; *T. thynnus* ($N=44$) 1.3–2.1, $\bar{x}=1.7$; *T. maccoyii* ($N=17$) 1.6–2.3, $\bar{x}=1.9$; *T. obesus* ($N=36$) 1.3–1.9, $\bar{x}=1.5$; *T. atlanticus* ($N=18$) 1.3–2.2, $\bar{x}=1.7$; *T. albacares* ($N=58$) 1.2–1.9, $\bar{x}=1.6$; *T. tonggol* ($N=4$) 1.4–1.8, $\bar{x}=1.6$. These proportions are close to those given by Godsil and Byers (1944: 86), who reported 1.7–3.0 for Pacific *T. alalunga* and 1.2–1.5 for Pacific *T. albacares*, and stated that Pacific *T. thynnus* and *T. obesus* are similar to *T. albacares*.

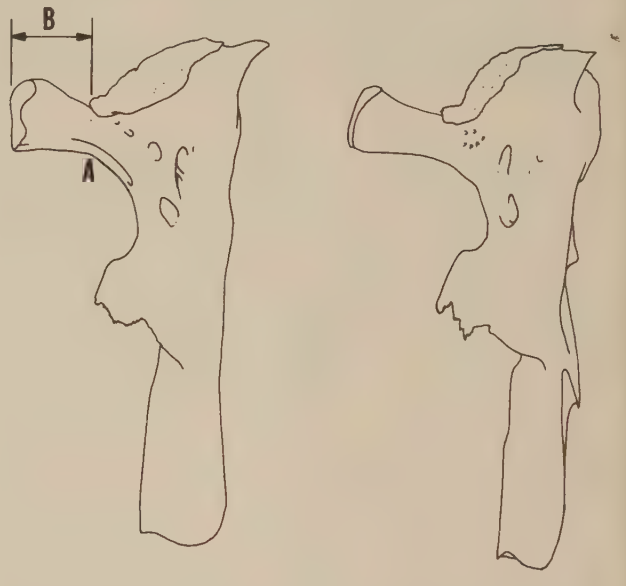


FIGURE 6.—Hyomandibula of (left) *Thunnus thynnus*, skull length 139 mm., (right) *T. alalunga*, skull length 150 mm. Measurements of anterior articular head include A—least width, B—length.

Kishinouye (1923: 322) stated that the anterior head is "more or less roundish in cross-section in *Thunnus;* but more or less flattened in *Parathunnus* and *Neothunnus*. . . ." We can find no significant difference among any of the species in this character. Furthermore, we cannot confirm de Sylva's contention (1955:14) that the process is oblique to the vertical limb in *T. atlanticus* but forms a right angle in the other species.

In *T. alalunga* the metapterygoid (fig. 7) is narrower than in other species. This condition can be indicated by the proportion of the length of the anteroventral margin to the posteroventral margin

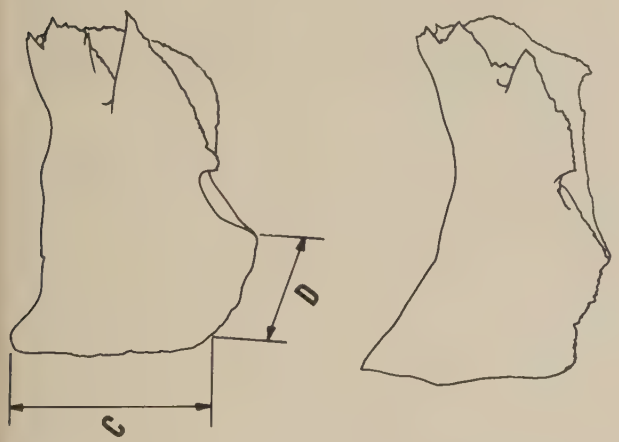


FIGURE 7.—Metapterygoid of (left) *Thunnus thynnus*, (right) *T. alalunga*, same specimens as in fig. 6, showing measurements of C—anteroventral margin, D—posteroventral margin.

(measured in each case to the midpoint of the arc of the posteroventral edge.) In our material, this proportion is as follows: *T. alalunga* ($N=32$) 1.1–1.8, $\bar{x}=1.4$; *T. thynnus* ($N=43$) 1.6–2.6, $\bar{x}=2.0$; *T. maccoyii* ($N=17$) 1.4–2.7, $\bar{x}=1.9$; *T. obesus* ($N=37$) 1.5–3.1, $\bar{x}=2.0$; *T. atlanticus* ($N=19$) 1.4–2.1, $\bar{x}=1.7$; *T. albacares* ($N=58$) 1.5–3.1, $\bar{x}=2.1$; *T. tonggol* ($N=4$) 1.8–2.2, $\bar{x}=2.0$. These proportions are similar to those given by Godsil and Byers (1944: 86) for Pacific tunas, but provide even better distinction. Godsil and Byers measured each margin to the "most ventral point," which seemed more nebulous to us than the midpoint of the arc. Their figures of 1.0–1.5 for *T. alalunga* and 1.3–1.9 for *T. albacares* and the other species include slightly lower proportions than were found in our specimens, but the conclusions are nevertheless similar.

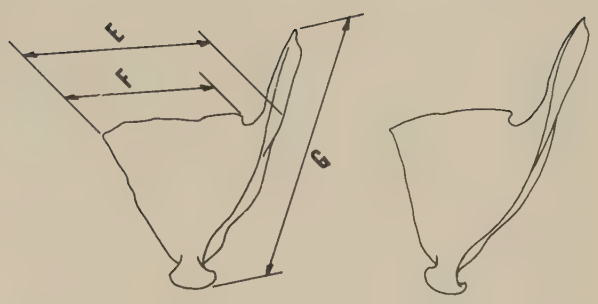


FIGURE 8.—Quadrate of (left) *Thunnus thynnus*, (right) *T. alalunga*, same specimens as in fig. 6, showing measurements of E—total width, F—width of horizontal edge, G—length.

Again, in *T. alalunga* the quadrate (fig. 8) is slightly narrower than in the other species. The proportion of length to total width in our specimens is as follows: *T. alalunga* ($N=35$) 1.5–2.1, $\bar{x}=1.8$; *T. thynnus* ($N=44$) 1.2–1.6, $\bar{x}=1.4$; *T. maccoyii* ($N=16$) 1.3–1.5, $\bar{x}=1.4$; *T. obesus* ($N=37$) 1.4–1.7, $\bar{x}=1.5$; *T. atlanticus* ($N=20$) 1.3–1.8, $\bar{x}=1.6$; *T. albacares* ($N=57$) 1.4–1.8, $\bar{x}=1.5$; *T. tonggol* ($N=4$) 1.4–1.6, $\bar{x}=1.5$. The proportions of the same length to width of the horizontal dorsal edge are: *T. alalunga* ($N=35$) 2.1–2.7, $\bar{x}=2.5$; *T. thynnus* ($N=44$) 1.6–2.1, $\bar{x}=1.9$; *T. maccoyii* ($N=16$) 1.6–2.0, $\bar{x}=1.9$; *T. obesus* ($N=37$) 1.8–2.2, $\bar{x}=2.0$; *T. atlanticus* ($N=20$) 2.0–2.3, $\bar{x}=2.1$; *T. albacares* ($N=57$) 1.8–2.2, $\bar{x}=2.0$; *T. tonggol* ($N=4$) 1.8–2.2, $\bar{x}=2.0$. We are not certain where Godsil and Byers (1944: 87) measured the width, but they gave proportions of 1.8–2.3 for Pacific *T. alalunga* and 1.6–1.8 for other species. Thus there is agreement in order of magnitude, but their proportions are generally higher than our first and lower than our second.

The subopercle of *T. thynnus* and *T. maccoyii* (fig. 9) differs, with few exceptions, from that of the other species in being relatively narrow and in having the anterodorsal margin almost vertical in its lower two-fifths to one-half, followed by a decided change in slope of the upper portion. In the other species there may be a very short perpendicular portion, less than one-fifth of the length, before the oblique slope begins, or, most often, there is an almost straight or very slightly convex oblique edge. This finding conforms with the observations of Godsil and Byers (1944: 101) for the Pacific forms and presumably also with the observations of Kishinouye (1923: 325), although his statement is less clear.

FIGURE 9.—Subopercle of (left) *Thunnus thynnus*, (right) *T. alalunga*. Same specimens as in fig. 6.

We are unable to confirm two other characters mentioned by Kishinouye (1923: 325, 327). In Japanese *T. thynnus* the posterior margin of the interopercle was described as being convex, whereas in other Japanese tunas it is nearly straight. In our material the shape of the margin is variable; most of the species have both types and variants thereof. Kishinouye also described a groove for blood vessels along the dorsolateral edge of the ceratohyal. The groove was present in *T. thynnus*, *T. alalunga*, and *T. obesus* but hardly visible in *T. albacares*. This grove is present in all species and is generally more apparent in larger specimens. In small specimens of most species the groove is indistinct or absent.

Pectoral and Pelvic Girdles

The pectoral girdle is composed of a series of bones connecting the skull and the pectoral fin. The two-armed supratemporal, not really a functional part of the pectoral girdle, is closely applied to the skin beside the otic region of the neurocranium. A larger, also two-armed, posttemporal articulates with the skull, followed by a supracleithrum and the large, curved, bladelike cleithrum. Baudelot's ligament runs from the supracleithrum to the basioccipital. From the posterior margin of the supracleithrum extend two flattened postcleithra, the second of which has an attenuated posteriorly directed process. The long curved blade of the cleithrum forms a thin-walled trough that opens posteriorly. The thickened, somewhat rectangular scapula is borne dorsally, on the mesial side. Below the scapula, the bladelike coracoid is attached. The lower, posterior end of the scapula and the uppermost posterior edge of the coracoid are thickened and flattened; they form articular surfaces for four pterygials, on which the fin rays are borne.

The pelvic girdle includes a pair of winglike basipterygia that join posteriorly in the median line. Anteriorly each bone has a flattened lateral wing and a long narrow mesial process. Posteriorly a long mesial process extends between the fin rays. There are no pterygials.

No differentiating characters are apparent in either the pectoral or the pelvic girdle.

Vertebral Column

General description.—Important papers describing the vertebral column in species of *Thunnus* include: Starks (1910), Kishinouye (1923), Frade (1932), Godsil and Byers (1944), Godsil and Holmberg (1950), Clothier (1950), de Sylva (1955), and Nakamura (1965).

The vertebral column usually has 39 vertebrae, including the hypural plate. The first vertebra is articulated firmly with the rear of the skull. Neural arches and spines are present on all except the hypural plate. The spines are erect and laterally flattened on the first six vertebrae. On the seven vertebrae anterior to the hypural plate, both the neural and haemal spines are wide and depressed and lie on top of the next posterior centrum, forming a strong and rigid tail section. Laterally directed transverse processes (parapophyses) appear as small projections on the third vertebra, become longest and broadest on about the sixth, shorter and more canted on the next two or so, and usually become both longer and ventrally directed on the eighth or ninth. By the 10th or 11th vertebra, the first closed haemal arch is formed by the meeting of the distal ends of the parapophyses. The ventral ends of the haemal arches become progressively longer, forming haemal spines. Ribs are attached, beginning with the 3d vertebra, to each parapophysis or to the end of each haemal arch or spine until the 18th or 19th vertebra. Posteriorly, haemal spines are present, but ribs are absent. Dorsal to the ribs, intermuscular bones (epipleurals) articulate either on the neural arch or the centrum of each of the vertebrae from the 1st to the 31st.

Beginning at the 12th to 18th vertebra, each haemal arch bears on each side a process directed obliquely ventrad which has been called a haemal prezygapophysis (de Sylva, 1955). On succeeding vertebrae this process is longer, then shorter and

more dorsally situated; by the 20th to 25th vertebra it comes to arise from the anterior end of the centrum rather than from the haemal arch.

Beginning at about the fourth vertebra, a process which has been called a haemal postzygapophysis (de Sylva, 1955) arises on each side from the posterior end of each centrum. On the anterior centra it is small and laterally directed. This process becomes ventrally directed on the eighth vertebra, and its distal end meets the parapophysis; farther posteriorly it meets the upper part of the haemal arch or the haemal prezygapophysis when it is formed. On approximately the last eight vertebrae the haemal spines are situated so posteriorly that they obliterate the haemal postzygapophyses.

From some or all of the 20th to the 33d vertebrae, the blood vessels and nerves that emerge from the haemal canal exit through ventrolateral foramina. The anterior foramina are formed by struts running from the haemal arch to the centrum near the base of the haemal postzygapophyses. They become smaller posteriorly and are separate from and anterior to the haemal arches; the latter in this region gradually become located toward the posterior end of the centra. On the 32d to 36th vertebrae, flattened lateral processes form a horizontal bony keel. The sizes of the individual vertebrae vary considerably, and regional differences are emphasized in older specimens. The length increases regularly to the 35th vertebra; the 36th is slightly shorter, the 37th and 38th are very short, and the 39th is incorporated into the wide, triangular hypural plate. The depth of the vertebra increases regularly to about the 25th, beyond which there is a gradual decrease to the hypural plate. A simple splintlike bone (epural) is closely applied to the anterodorsal surface of the hypural plate. A similar bone (hypural) bearing a spinous process on each side is present along the anteroventral surface of the hypural plate. The terminology and derivation of these two bones are in doubt.

Specific Characters.—The vertebrae typically total 39 in all species. Godsil and Byers (1944) reported, and we have reexamined, a California *T. thynnus* with only 38, in which 1 vertebra near the hypural is obviously missing. Among more than 200 skeletons of the seven species, we found only three additional abnormalities, all due to recognizable fusion of two adjacent centra. Frade (1932) reported, among 110 *T. thynnus*, 8 with 38 vertebrae, 6 with 40, and 1 with 41. We doubt the counts of 40 and 41 but cannot explain them. All but one species have 18 precaudals and 21 caudals, the first long haemal spine occurring on the 19th vertebra. The same count was given by de Sylva (1955) for *T. atlanticus*, but, as Watson (1964) has shown, this species differs from all other *Thunnus* in having 19 precaudals and 20 caudals. Exceptions may be expected in all species; we have examined *T. atlanticus* with counts of 18+21 and 20+19, *T. obesus* and *T. albacares* with 17+22, and *T. thynnus* and *T. obesus* with 19+20; and Godsil and Byers (1944: 86) reported one *T. alalunga* with 20+19.

The position of the first (anteriormost) ventrally directed parapophyses appears to show almost no variability within a species or subspecies; only one exception has been noted. These parapophyses occur on the 8th vertebra in *T. thynnus*, on the 10th in *T. tonggol*, and on the 9th in the other species. In *T. alalunga* none of the parapophyses is directed quite so obviously ventrad as in the other species; those on the ninth vertebra that we regarded as ventrally directed are much shorter than in any other species and seem almost twisted, never becoming completely ventrally oriented. In other species, there is variation in the ventral extent of the preceding parapophyses. As long as these were more or less flattened and rounded, their relative location was not considered. The first ventrally directed ones are definitely elongated in a ventral direction (compare the eighth vertebra in *T. thynnus* and *T. maccoyii*, fig. 10).

The first (closed) haemal arch usually occurs on the 11th vertebra in *T. albacares*, *T. atlanticus*, *T. tonggol*, and *T. obesus*, and usually on the 10th vertebra in *T. alalunga*, *T. maccoyii*, and *T. thynnus*. In all species except *T. alalunga* and *T. maccoyii* we observed the first closed arch occasionally either one vertebra anterior or one vertebra posterior to the usual position. Godsil and Byers (1944: 68, 101) observed notable variation in Pacific *T. albacares* and in *T. thynnus*. In most of the species the parapophyses on the vertebra preceding the one that bears the first haemal arch approach each other so closely in the median line that it appears to be a matter of chance whether or not they or the next pair fuse. In many specimens in which the haemal arch was formed anterior to its usual position, its shape was noticeably different (fig. 10, OBE).

In *T. alalunga* the first haemal arch is directed forward, with an angle of about 45° or less between it and the vertebral axis. In all of the other species

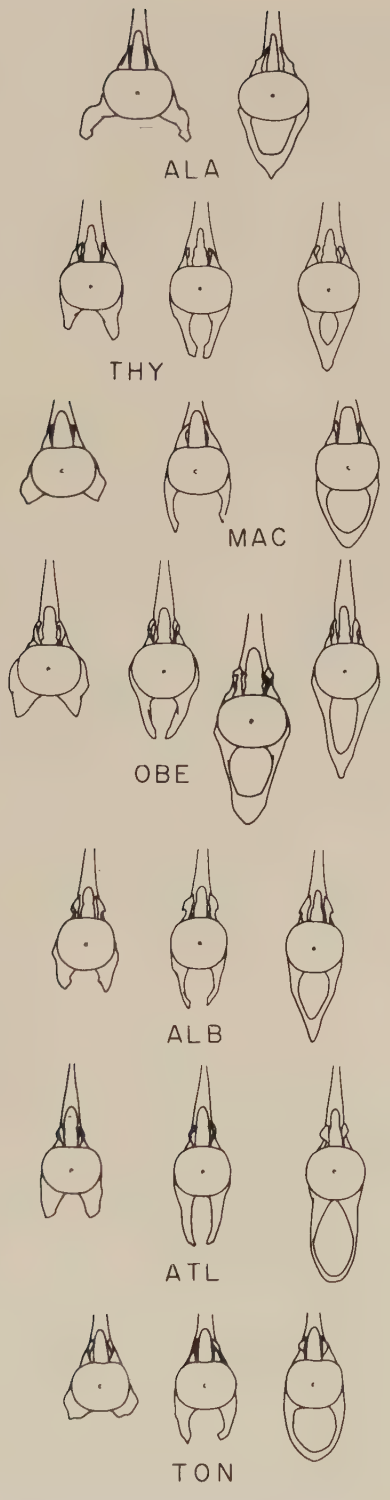


FIGURE 10.—Anterior view, first closed haemal arch and preceding vertebrae of *Thunnus* species. ALA—vertebrae 9–10, ALB—9–11, ATL—9–11, MAC—8–10, OBE—9–11 (the one slightly below the main row shows shape of first closed haemal arch when located on 10th vertebrae), THY—8–10, TON—9–11.

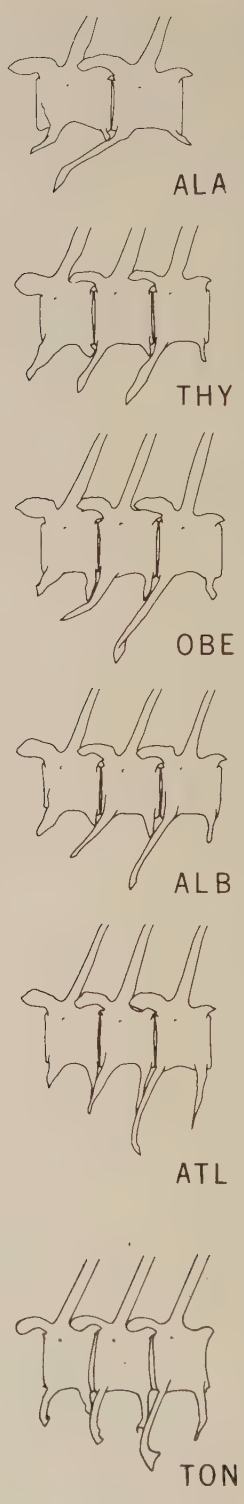


FIGURE 11.—Left lateral view of vertebrae of *Thunnus* species showing first ventrally directed parapophyses (left vertebra) and first closed haemal arch (right vertebra). ALA—vertebrae 9–10, ALB—9–11, ATL—9–11, OBE—9–11, THY—8–10, TON—10–12.

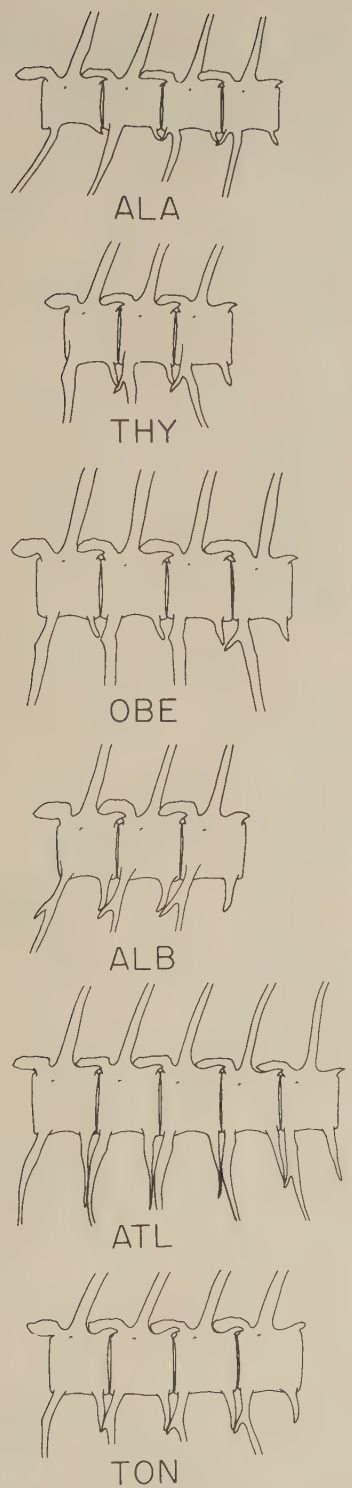


FIGURE 12.—Left lateral view of vertebrae of *Thunnus* species, showing development of anteriormost haemal pre- and postzygapophyses. ALA—vertebrae 13–16, ALB—14–16, ATL—14–18, OBE—14–17, THY—14–16, and TON—14–17.

it may range from almost perpendicular to a 60° angle (fig. 11). The shape of the first haemal arch and the dimensions of its bony parts vary considerably, but in *T. atlanticus*, *T. tonggol*, and *T. maccoyii* the bony portions are thinner and the sides more bowed than in the other species (fig. 10).

As shown by Yabe et al. (1958), by Matsumoto (1963), and by Yoshida (1965), the heamal spine of the first caudal vertebra is always laterally flattened and winglike in *T. alalunga* but in the other species resembles the other haemal spines and is not flattened.

The length of the haemal prezygapophyses and the distance of their origin from the centrum vary among the species of *Thunnus*. In *T. alalunga* the haemal prezygapophyses all originate at the centrum or extremely close to it. Correlated with this, the anterior haemal postzygapophyses are relatively short (fig. 12). In the other species the anterior haemal prezygapophyses arise from the sides of the haemal arches of 3 to 12 vertebrae before they begin to arise from the centra, and the posterior haemal postzygapophyses are relatively longer. In *T. alalunga*, *T. obesus*, *T. maccoyii*, and *T. thynnus* the haemal prezygapophyses arise high on the neural arch, so that only the first two or three at most can be regarded as clearly on the arch. Correspondingly, the associated haemal postzygapophyses hardly differ in length from those on the posterior vertebrae. By contrast, in *T. atlanticus*, *T. albacares*, and *T. tonggol* the haemal prezygapophyses arise far more ventrad on the haemal arch, from one-fourth to one-half the distance to the ventral tip, and there is no question that at least five (usually more) are definitely on the arch, not on the centrum. The associated haemal postzygapophyses in these species are longer than in the other three, although less so in *T. albacares* than in *T. atlanticus* and *T. tonggol*. In *T. atlanticus* and *T. tonggol* the longest haemal postzygapophyses are equal to or longer than the length of the centra; in *T. albacares* they may be about three-fourths the centrum length.

The species differ in the development of the ventrolateral foramina that are found on some or all of the 20th to the 33d vertebrae (fig. 13). These foramina are best developed anteriorly and in this region appear to arise through the formation of a bony strut from the haemal postzygapophyses to the dorsal part of the haemal arch. They diminish in size posteriorly and are absent on the last several vertebrae. In *T. atlanticus*, *T. albacares*, and *T. tonggol* the anterior openings are large, longer than wide,

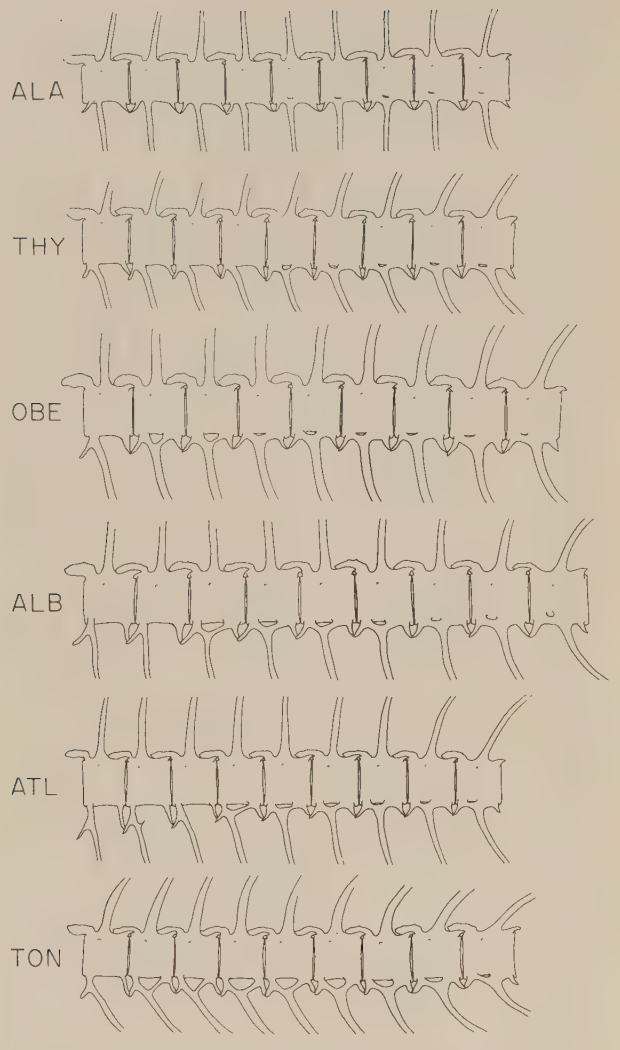


FIGURE 13.—Left lateral view of vertebrae 20–28 of *Thunnus* species, showing development of inferior foramina.

the largest usually three times or more as long as the horizontal width of the base of the corresponding haemal spine. In *T. obesus*, *T. maccoyii*, *T. thynnus*, and *T. alalunga* the size of the openings is variable, usually small, and the largest opening is rarely more than about 1.5 times as long as the width of the adjoining bony neural arch.

T. atlanticus, *T. albacares*, and *T. tonggol* are distinguishable by the development of vertebral processes and openings, which approach the ornate trelliswork seen in *Auxis*, *Euthynnus*, and *Katsuwonus; T. alalunga* shows the least development, and *T. obesus*, *T. maccoyii*, and *T. thynnus* are intermediate.

The first haemal prezygapophysis tends to be found more anteriorly in *T. albacares* and *T. tonggol*, most commonly on vertebra 13 or 14 (range 12–15) in *T. albacares*. In *T. maccoyii* it usually occurs on 14 or 15 (range 14–16), in *T. alalunga* and *T. obesus* on 15 or 16 (range 14–17), and in *T. atlanticus* on 16 or 17 (range 15–18). *T. thynnus* displays a wider range of variation (12–17), and overlap is considerable between it and the other species.

While this paper was in press, Nakamura and Kikawa (1966) described specific differences in the infra-central grooves on the ventral side of the centra of vertebrae 10-30. These infra-central grooves were categorized into three types: type A with two separate infra-central grooves; type B with two grooves connected by a canal; type C with a single, usually elongate, groove. We have reexamined our skeletal material, which comprises many more specimens than the total of 19 used by Nakamura and Kikawa, and we conclude that the infra-central grooves are a useful character, but show variation that often precludes positive species identification. Our conclusions are as follows:

Thunnus albacares (24 specimens, fork length 280-1,430 mm.) has type C infra-central grooves that tend to be divided by a thin septum anteriorly but that posteriorly are undivided or occupied by a honeycomb-like network of bony material. In this character, *T. albacares* is distinctive, but is approached by some specimens of *T. maccoyii*.

Thunnus maccoyii (16 specimens, 742-1,445 mm.) is the most variable of all the species. Very few have type C (undivided) grooves, as described by Nakamura and Kikawa. Typically, all the vertebrae have two grooves (type A) that are divided by very thin septa or a honeycomb of septa. This condition resembles that of the anterior grooves of *T. albacares*. Only an occasional undivided groove occurs among the divided ones in *T. maccoyii*, whereas most of the grooves are undivided in *T. albacares*. Some specimens, particularly the six from Australia that were used by Godsil and Holmberg (1950), were almost impossible to distinguish from *T. thynnus*.

Thunnus thynnus thynnus (7 specimens, 316-2,315 mm.) and *T. t. orientalis* (18, 530-1,450 mm.) have type A grooves, two grooves per centrum, that tend to be round or oval anteriorly and become longer and narrower posteriorly. The distance between the two grooves on the anterior centra is highly variable. When the grooves are narrowly separated, the specimens resemble some *T. maccoyii*.

Thunnus obesus (7 Atlantic specimens, 697-1,360 mm.; 3 Indian Ocean, 630-1,270 mm.; 1 eastern Pacific, 1,600 mm.) have type A grooves and could not be distinguished from *T. thynnus*.

Thunnus alalunga (20 specimens, 520-1250 mm.), like *T. thynnus* and *T. obesus*, have type A grooves, but, although the grooves vary greatly in width, they tend to be much narrower than in the latter two species. Usually the grooves are widely separated, but in a few specimens, the partitions are narrow.

Thunnus tonggol (4 specimens, 373-924 mm.) have type B grooves, two grooves per centrum, quite variable in size, with a shallow canal connecting them. The grooves tend to be larger than those of *T. atlanticus* and smaller than those of *T. thynnus* or *T. obesus*. In the two larger specimens, the anterior grooves strongly resemble those of *T. thynnus* or *T. obesus* in being larger and close together.

Thunnus atlanticus (20 specimens, 322-665 mm.) have type B grooves, with two very small pits on each centrum connected by a very narrow canal. The canal is not evident in some specimens, giving the impression that the two grooves are separated by a sharp ridge. In this respect *T. atlanticus* is distinctive. The largest specimens, however, closely resemble small *T. tonggol*, with small grooves connected by an obvious canal, the grooves becoming elongate posteriorly.

The proportion of length to depth of the 36th vertebra is relatively greatest in *T. albacares* ($N=60$) 1.2–1.9, $\bar{x}=1.4$ and in *T. alalunga* ($N=40$) 1.1–1.7, $\bar{x}=1.5$. In *T. alalunga* the vertebrae are often considerably smaller anteriorly than posteriorly (fig. 14), accounting for the high ratio. In the other species, this proportion is: *T. thynnus* (N=58) 0.8–1.3, $\bar{x}=1.1$; *T. maccoyii* ($N=16$) 0.8–1.3, $\bar{x}=1.0$; *T. obesus* ($N=30$) 0.9–1.4, $\bar{x}=1.2$; *T. atlanticus* ($N=23$) 1.0–1.4, $\bar{x}=1.3$; *T. tonggol* ($N=8$) 1.1–1.5, $\bar{x}=1.3$.

VISCERA

The relative position, shape, and size of the various internal organs provide excellent diagnostic characters (fig. 15). These organs are treated here by systems. Important works on the viscera of *Thunnus* include those of Eschricht and Müller (1837), Kishinouye (1923), Frade (1925), Serventy (1942), Godsil and Byers (1944), and Godsil and Holmberg (1950).

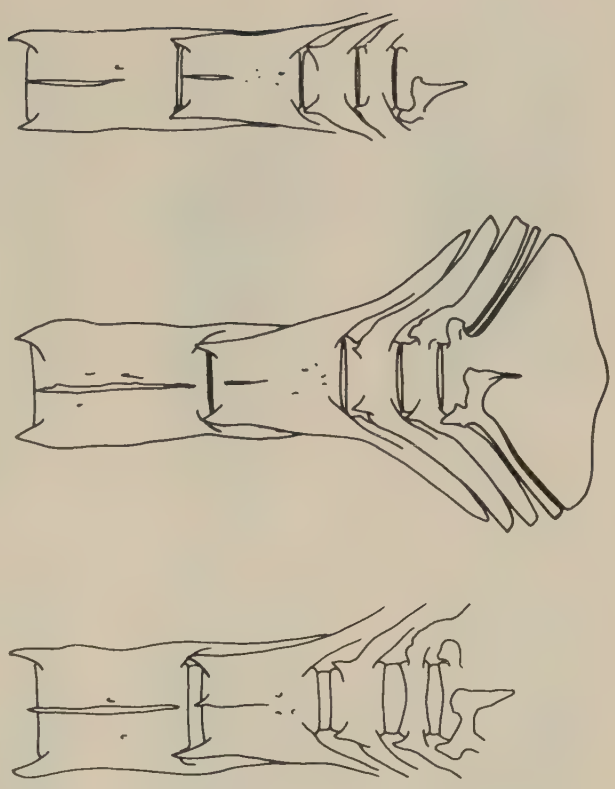


FIGURE 14.—Left lateral view of vertebrae 35–39, showing differences in proportions of vertebra 36. (top) *Thunnus albacares*, (middle) *T. alalunga*, (bottom) *T. obesus*, typical of other species not illustrated.

Digestive System and Associated Organs

General Description.—At the anterior end of the body cavity the liver abuts against the transverse septum and caps the other organs. It is usually composed of three lobes, only the middle of which is plainly visible in ventral view; the other two lobes lie along the lateral body wall, hidden by the other organs. The ventral surface of the liver of some species appears striated owing to the parallel arrangement of blood vessels (both arterial and venous) near its surface. The species with striated livers also possess, on the dorsal surface of the liver, several large "vascular cones," each comprising numerous vessels bound in a common sheath. These are absent in species with unstriated livers. In all species (Morice, 1953, to the contrary) there are two efferent (venous) vessels leading directly from the anterior surface of the liver into the sinus venosus. The esophagus merges indistinguishably (in external view) into the stomach, which forms a blind sac posteriorly. The intestine rises from the anterior

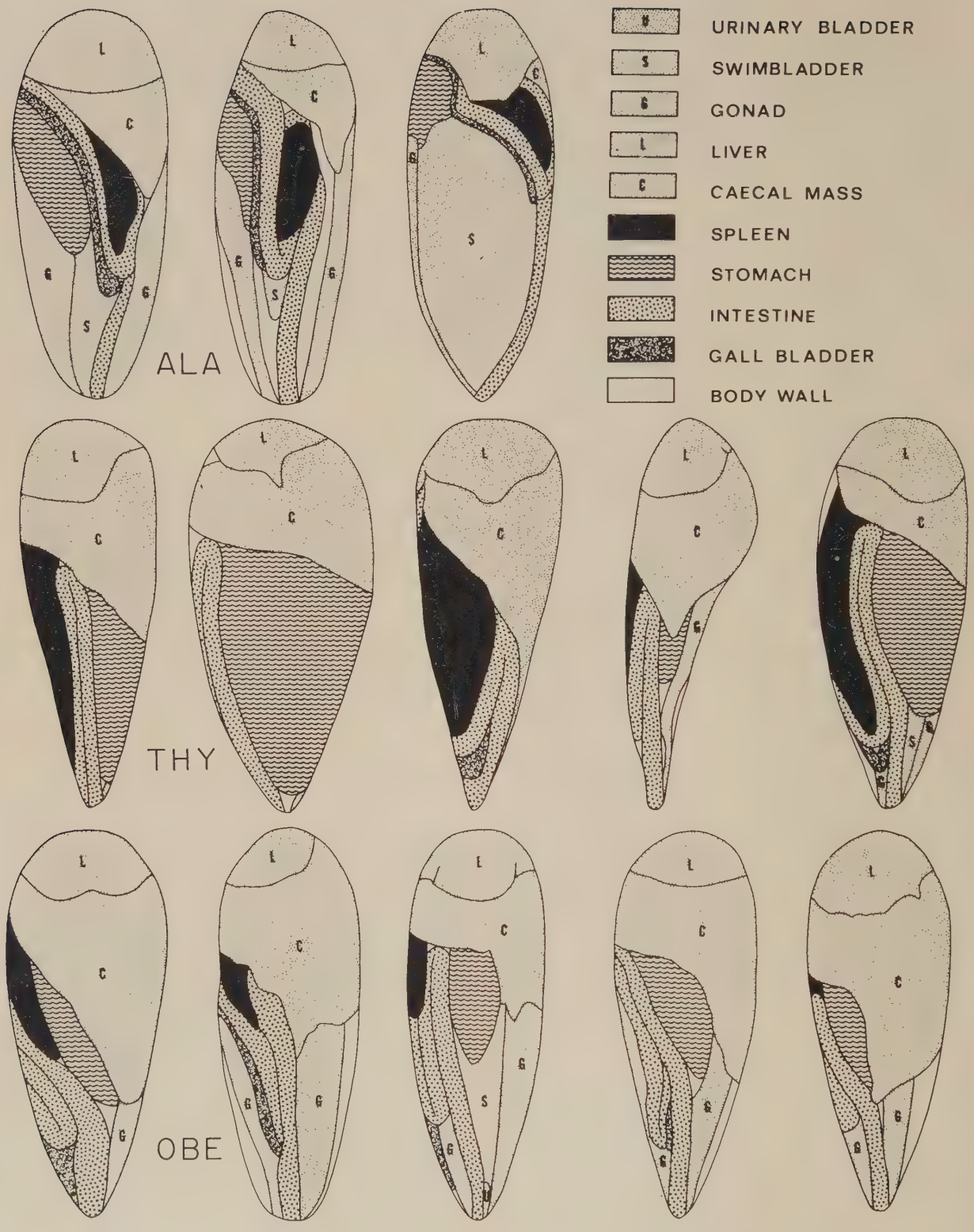
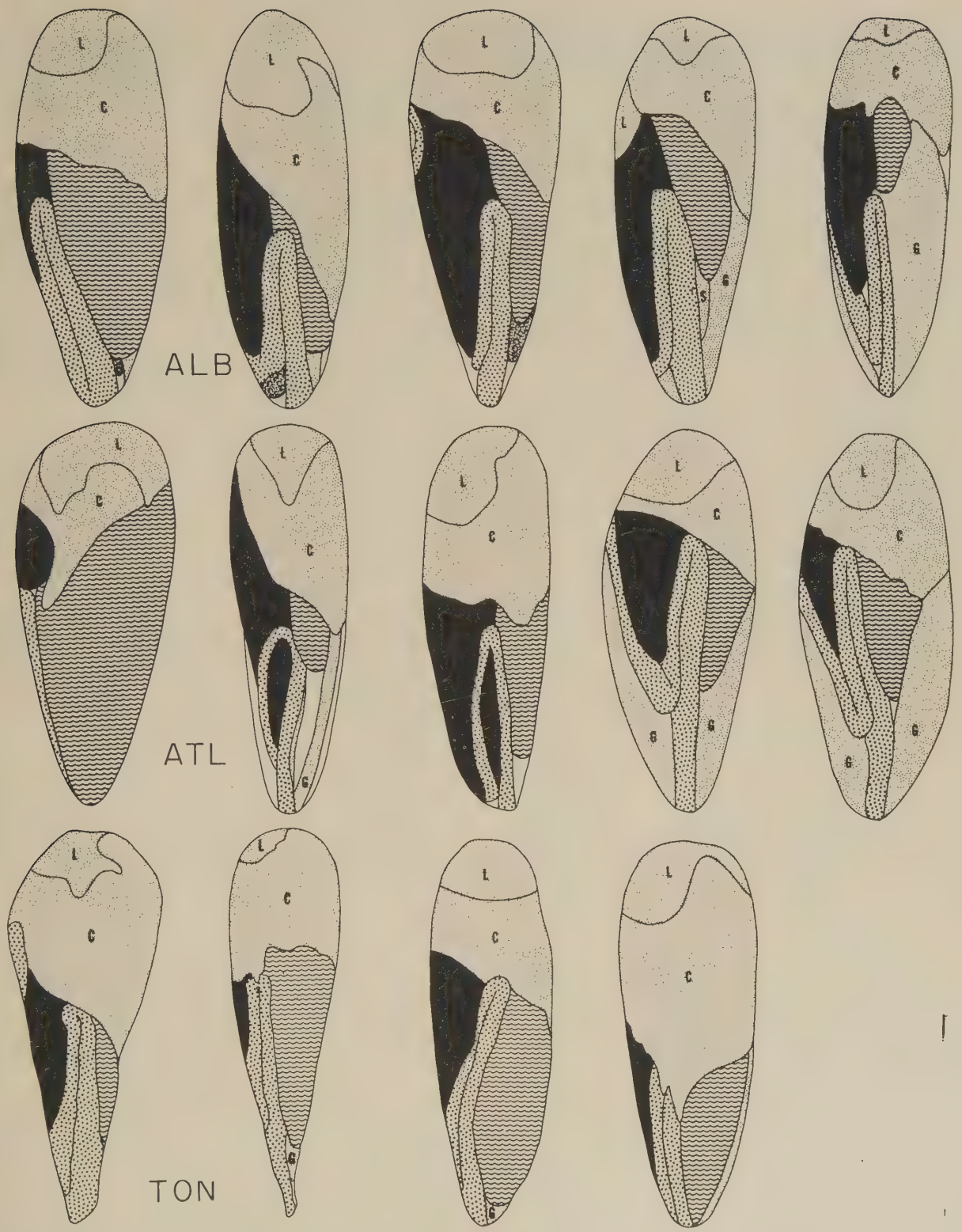


FIGURE 15.—Ventral view of in situ visceral patterns of *Thunnus* species. Arranged from left to right in order of increasing fork length. ALA—780, 875, 1,030 mm.; ALB—637, 700, 808, 1,340,



1,420 mm.; ATL—337, 438, 513, 563, 650 mm.; OBE—1,250, 1,310, 13,50 1,450, 1,540 mm.; THY—457, 750, 872, 1,050, 1,670 mm.; TON—373, 392, 910, 924 mm.

end of the stomach, and a very large caecal mass is attached to its origin by several ducts that are not externally apparent. The intestine proceeds caudad for half or more the length of the body cavity (straight intestine), forms a loop, runs craniad (ascending portion) almost to the pylorus, then forms another loop and continues in a nearly straight line (descending portion) to the anus. The spleen is located between the straight and ascending portions. The gall bladder is a long, tubular sac rising from the right lobe of the liver, attached to the dorsal wall or the left side of the straight intestine. A swim-bladder, when present, is situated dorsad to the main visceral mass, and may be rudimentary or well developed.

Specific Characters.—The ventral surface of the liver (fig. 16) is striated in *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus*. These striations give the impression of being denser and extending farther toward the center of the middle lobe in *T. alalunga*, *T. maccoyii*, and *T. thynnus* than in *T. obesus*, but this difference is not easy to detect. We have seen only one instance of striations being limited to the peripheral margins, at least of the middle lobe, as described by Kishinouye (1923) and Godsil and Byers (1944) for Pacific, and by Morice (1953) for Atlantic *T. obesus*. The peripheral nature of these striations has been used as a major diagnostic character of the nominal genus *Parathunnus*. In *T. albacares*, *T. atlanticus*, and *T. tonggol* the liver lacks striations.

In *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus* the three liver lobes are subequal in length, the lateral lobes most often slightly shorter than the middle lobe. In *T. albacares*, *T. atlanticus*, and *T. tonggol* the right lobe is much longer and narrower than the middle or left lobe.

Correlated with the ventral striations on the livers of *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus*, vascular cones are associated dorsally with each lobe. The middle lobe always has a single large cone; the other lobes usually have two or more, and these may be somewhat difficult to distinguish from ordinary blood vessels. In the left lobe, we recorded two to five cones in *T. alalunga;* two to six, usually two or three, in *T. thynnus;* two to four in *T. maccoyii;* one to six, usually one or two, in *T. obesus*. In the right lobe we found: two to eight, usually two, in *T. alalunga;* one or two, usually two, in *T. thynnus;* two in *T. maccoyii;* one to four, usually one or two, in *T. obesus*.

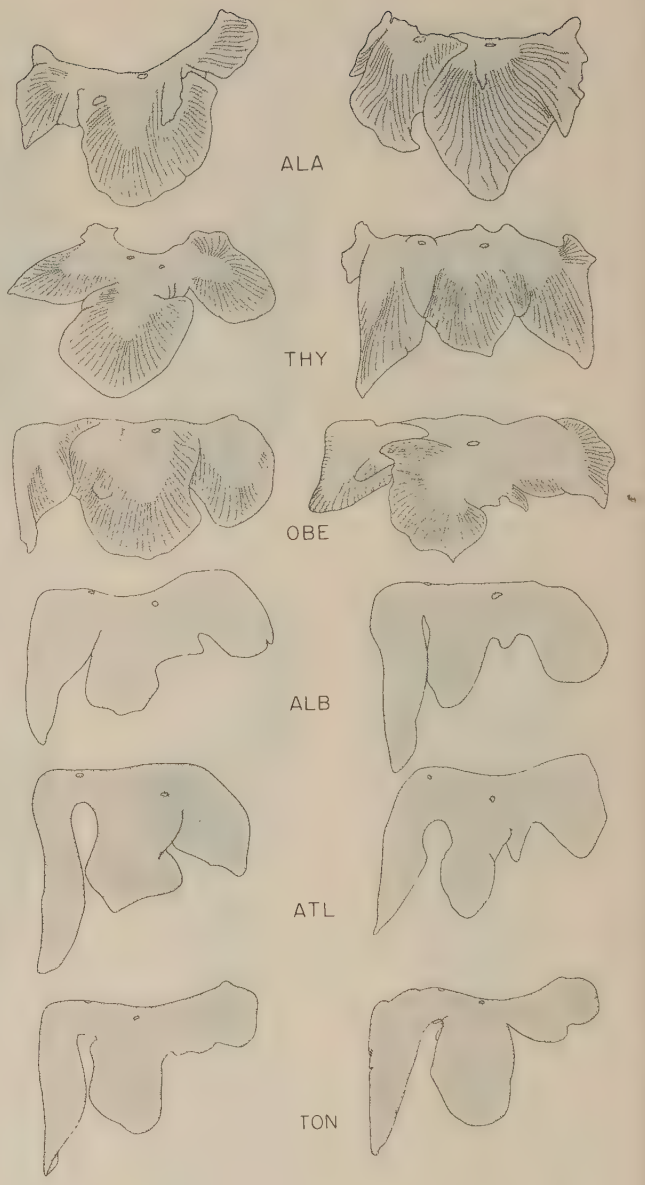


FIGURE 16.—Ventral view of livers of *Thunnus* species, showing shape and presence or absence of striations. Fork lengths (left, right): ALA—875, 1,030 mm.; ALB—700, 1,175 mm.; ATL—568, 650 mm.; OBE—1,450, 1,540 mm.; THY—457, 757 mm.; and TON—910, 924 mm.

Morice (1953) described the liver of *T. albacares* as having two efferent vessels at the anterior end, but noted only a single vessel in *T. alalunga*, *T. thynnus*, and *T. obesus*. He probably overlooked the vessel in the right lobe near the junction with the middle lobe, because this vessel is smaller than the one in the middle lobe. All specimens that we examined had two such efferent vessels.

Thunnus alalunga has the spleen on the left side and the stomach on the right. In the other species these positions are reversed (fig. 15).

Godsil and Byers (1944) attached considerable importance to their observation that the straight intestine in *T. alalunga* crosses from the right to the left side, and the descending portion lies on the left side. This course is obviously correlated with the position of the stomach in this species. We found that the intestine often does not cross over so obviously and that the descending portion is commonly near the middle. Thus there is little or no difference between *T. alalunga* and the other species in position of the descending intestine, although the side on which the intestine originates is different.

The relative position of the first loop of the intestine (where the straight intestine forms the ascending portion) differs to a degree among the species (fig. 15). In *T. alalunga* this loop is shortest and is located about one-half to two-thirds the distance between the posterior margin of the middle liver lobe and the anus. In the other six species the loop may reach from about three-fourths to nine-tenths of the liver-anus distance. In Pacific forms, *T. alalunga* is reported by Godsil and Byers (1944) to have a short "fold" (27–41 percent of body cavity), *T. albacares* a slightly longer "fold" (36-61 percent), and *T. thynnus orientalis* and *T. obesus* a long "fold." Their illustrations and measurements, and our observations, indicate such a wide range of variation that only *T. alalunga* can be regarded as distinct in this character.

One Atlantic specimen of *T. obesus* among our study material had two intestinal loops, a situation never before reported to our knowledge.

The length of the spleen (fig. 15) is normally short, seldom reaching beyond half the distance from caecal mass to end of body cavity in *T. alalunga*, *T. obesus*, and *T. atlanticus*, but usually long, reaching at least three-fourths of this distance in *T. thynnus*, *T. maccoyii*, and *T. albacares; T. tonggol* is variable. In all species there are exceptions.

The gall bladder (fig. 15) in *T. alalunga* is normally exposed along the entire right side of the straight intestine. In the other species it is usually either entirely hidden or a small portion may appear posterior to the first intestinal loop; in the few specimens in which it was largely exposed, the visceral mass seemed to be distorted.

The swimbladder (fig. 17) appears to be invariable and distinctive only in *T. obesus*, in which it is long, usually slender, beginning near the transverse septum, and tapering to a point that reaches the posterior end of the body cavity.

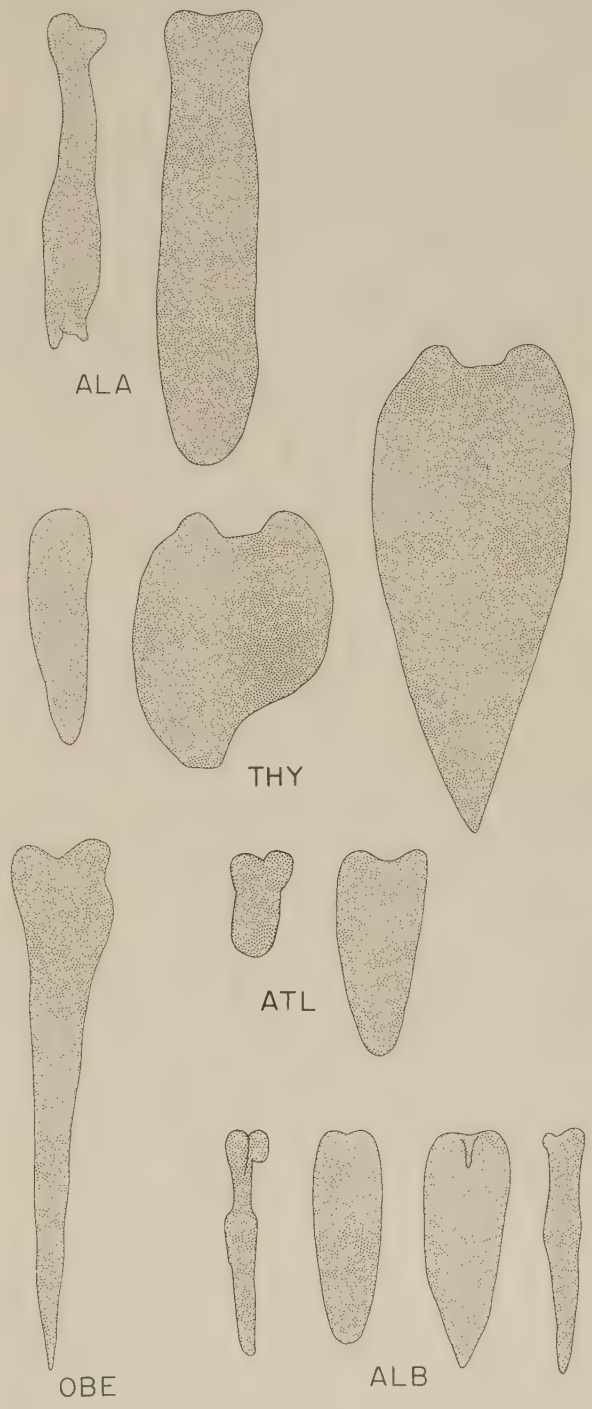


FIGURE 17.—Ventral view of swimbladder shapes of *Thunnus* species. Fork lengths (left to right): ALA—875, 1,030 mm.; ALB—637, 700, 1,175, 1,420 mm.; ATL—650, 664 mm.; OBE—1,250 mm.; and THY—954, 1,050, 1,670 mm.

Absence of a functional swimbladder in *T. tonggol* may be regarded as a useful diagnostic character, but in most specimens we discovered a tiny swimbladder, about 4 mm. in diameter, which could easily have been overlooked. A very small swimbladder (ca. 20 mm. long) also was present in two *T. maccoyii* (742 and 764 mm.).

Variation in the other five species is considerable (fig. 17). In *T. atlanticus* the swimbladder may be short, oblate, lying far anterior in the body cavity; or it may approach the length of a poorly developed swimbladder of *T. albacares*. In the latter case, the swimbladder is comprised of two chambers divided by a transverse membrane, with the anterior chamber probably representing the small type of swimbladder, the posterior chamber an addition. In *T. albacares* the swimbladder is moderately long, usually reaching about the level of the 14th or 15 vertebra (range 12–17). In *T. alalunga* it varies from narrow, only moderately long, and deflated, to fully the length of the body cavity and inflated to fill much of the cavity.

In *T. thynnus* and *T. maccoyii* variation in swimbladder dimensions may be correlated with growth. The changes in swimbladder dimensions were recognized by Serventy (1956a:10), and were suggested but not recognized by Godsil and Holmberg (1950: 21). Smaller specimens (457–954 mm.) have rudimentary swimbladders that are slender, deflated, and short (about 6 vertebrae long), about a quarter of the length of the body cavity, and do not reach the depression anterior to the dorsal bulge. In two *T. maccoyii* the swimbladder was tiny and could easily have been missed in a casual dissection. In a 1,060-mm. specimen of *T. t. thynnus* the organ was inflated and occupied about half the body cavity (fig. 17). In specimens 1,390-mm. and larger the swimbladder extends from the depression anterior to the kidney almost or quite to the posterior end of the body cavity; it is as wide as the body cavity in its anterior half and posteriorly tapers almost to a point.

Urogenital System

General Description.—The paired gonads are frequently visible in ventral view. They lie along the dorsolateral body wall, their posterior ends forming ducts which open on each side of the urinary papilla. The kidney is anterior in position and dorsal to the layer of fibrous connective tissue overlying the swimbladder. Its anterior margin usually follows the edges of the depression anterior to the hump formed by the haemal arches, and lateral extensions reach forward in a semicircle and sometimes nearly meet anteriorly. Depending upon the species, a posterior extension ("tail") may reach about as far as the level of the 16th vertebra; and *T. albacares* sometimes has accessory masses of kidney tissue posterior to the main mass. In the anterolateral extensions of the kidney, the urinary ducts ("ureters") arise and join within or just posterior to the kidney substance, and the resulting single duct proceeds posteriorly. Just before the anus, the duct enters a small but prominent urinary bladder, which may lie within the mesenteries of the gonads or project freely into the body cavity, depending upon the species. The urinary bladder empties through a urinary papilla behind the anus.

Specific Characters (fig. 18).—The kidney of *T. alalunga* is unique in lacking a "tail," the end reaching the level of the 7th to 9th vertebra (11th in one specimen). In *T. thynnus* and *T. maccoyii* the tail is relatively short, reaching the 8th to 11th vertebra. Its configuration varies in Atlantic specimens from tapering to truncate, encompassing all the forms used by Godsil and Holmberg (1950) to differentiate *T. maccoyii* from Atlantic and Pacific *T. thynnus*. None of our *T. maccoyii* had truncate kidneys. In *T. obesus* the tail is slightly longer than in *T. thynnus*, reaching the 11th to 14th vertebra, is narrower, and is more distinctly delimited from the anterior kidney mass. The kidney of *T. albacares* has a long tail, tapering gradually from the anterior kidney mass and reaching the 12th to 16th vertebra; accessory kidney masses are often present posteriorly. In *T. atlanticus* the kidney mass is bulky anteriorly and has a long, narrow tail that reaches the 12th to 17th vertebra. In *T. tonggol* there is a large anterior portion and a long, narrow tail that reaches the 15th to 17th vertebra.

The branching of the ureters varies considerably, but shows some general tendencies that, together with the shape of the kidney, are useful in distinguishing species (fig. 18). In the tailless kidney of *T. alalunga*, the two main branches are widely divergent, joining at the posteriormost end of the kidney substance. In *T. thynnus* and *T. maccoyii* the junction may occur at the posterior end, at some distance craniad, or just posterior to the kidney. The angle formed by the branches is small when the junction is well posterior, large when far anterior. In *T. obesus* the branches converge to run close together and almost parallel for a considerable dis-

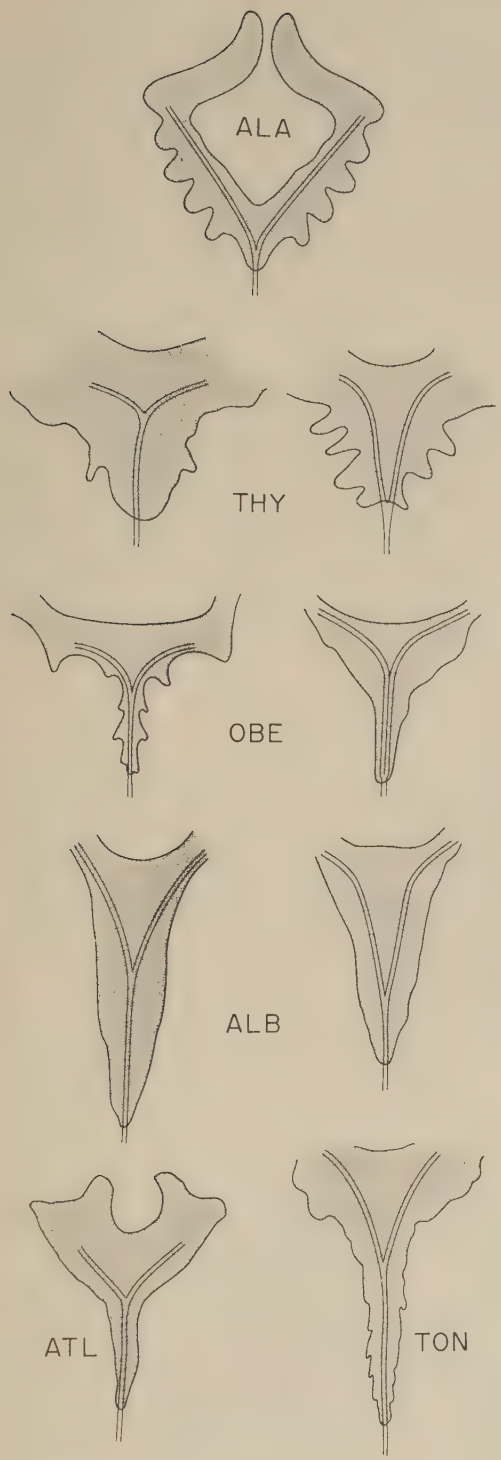


FIGURE 18.—Ventral view of kidney and ureter of *Thunnus* species. Forward extent shown only in ALA and ATL. Fork lengths (left, right): ALA—875 mm.; ALB—700, 1,175 mm.; ATL—533 mm.; OBE—1,310, 1,350 mm.; THY—457, 872 mm.; and TON—910 mm.

tance before they join at the posterior end of the kidney. In those specimens in which the junction occurs well forward, the angle between the branches is less than in *T. thynnus* or *T. maccoyii*. In *T. albacares* and *T. tonggol* the branches usually converge gradually, at a very slight angle, and join at some distance craniad from the end of the kidney tail. When the junction is almost at the posterior end of the tail, the branches may be almost parallel for a short distance. The junction of the branches in *T. atlanticus* usually occurs far anteriorly, and the angle between the branches is usually large. Some specimens, however, resemble *T. albacares*.

Our observations on the urinary bladder are few, but they suggest more variation than was implied by Godsil and Byers (1944). The extent to which the bladder is embedded in the dorsal body wall or projects freely into the body cavity seems to be partly a matter of interpretation. In all species, most of the bladder was contained in the membrane between the left and right gonads. Some *T. thynnus* and *T. alalunga* had much of the posterior part closely attached to the body wall, but the anterior part was separated from the body wall and contained in the membrane of the gonads. The anterior tip of the bladder actually projected free of the membrane in some specimens of *T. obesus*. In all three of these species, at least some specimens had the bladder, except for its posteriormost end, entirely within the membrane, not attached to the body wall, and without a freely projecting anterior tip; this was the only condition observed in the other four species.

Dorsal Connective Tissue

Covering most of the dorsal body wall, dorsal to the peritoneum but ventral to the kidney, is a region of tough, white fibrous connective tissue. In *T. alalunga* the sheet becomes extremely thick posteriorly. In *T. albacares* a thick raised median cord forms in the anterior half. The other species have a rather uniform thin sheet of tissue, perhaps slightly thickened posteriorly.

VASCULAR SYSTEM

Important papers on the circulatory system of *Thunnus* include those of Kishinouye (1923), Godsil and Byers (1944), and Godsil and Holmberg (1950).

General Description

The pericardial cavity is separated from the pleuroperitoneal cavity by a transverse septum, the walls

of which are formed posteriorly by peritoneum, anteriorly by pericardium and the walls of the sinus venosus and the ducts of Cuvier, which enter the sinus. No specific differences have been observed in these structures or in the heart itself.

After leaving the heart, blood is carried in the ventral aorta, which sends an afferent branchial artery into each of the gill arches. After circulating in the capillaries of the gill lamellae, the blood from each gill arch enters an efferent branchial (epibranchial) artery. The anterior two epibranchials of each side unite to form a common trunk, and these trunks join as the "Y" of the aorta, usually beneath the second vertebra, to form the dorsal aorta (fig. 19). The posterior two epibranchials of each side also unite, and their short common trunks join the dorsal aorta, usually beneath the third vertebra. The dorsal aorta continues posteriorly along the dorsal body wall to the first haemal canal. The coeliaco-

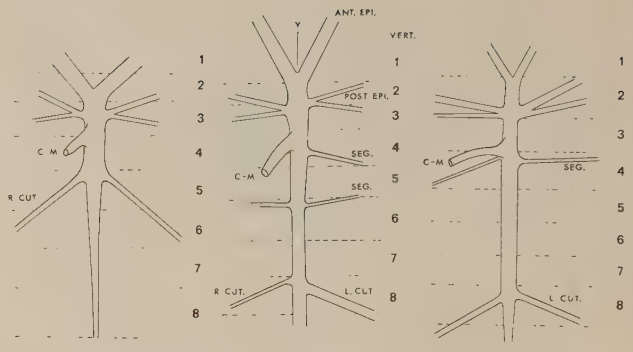


FIGURE 19.—Representative patterns of anterior branches of dorsal aorta in *Thunnus* species. (Left) *T. alalunga;* (middle) *T. atlanticus;* (right) *T. tonggol.* Y: Y of aorta. ANT EPI: anterior epibranchials. POST EPI: posterior epibranchials. C–M: coeliaco-mesenteric. SEG: segmental. L. CUT and R. CUT: Left and right cutaneous. VERT: vertebrae separated by dashed lines.

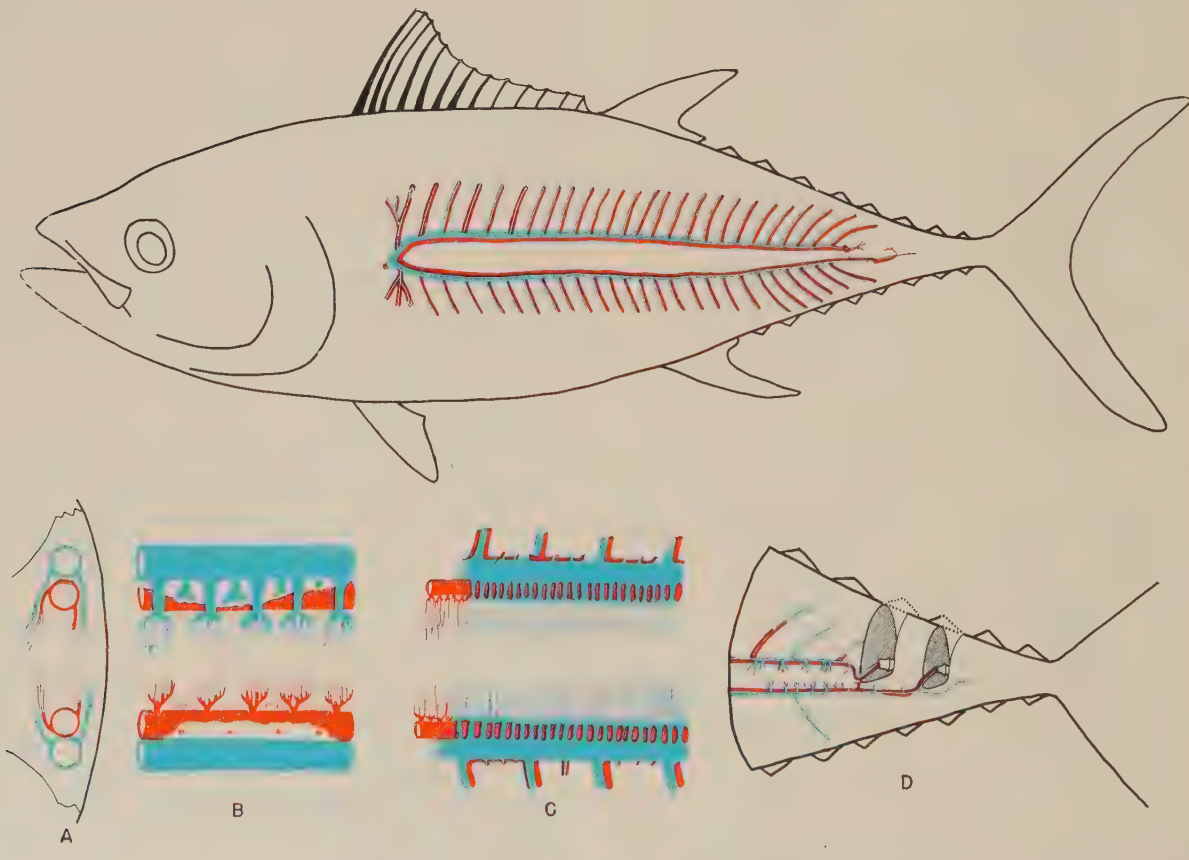


FIGURE 20.—Cutaneous system of arteries (red) and veins (blue) of *Thunnus obesus.* (upper) Course of cutaneous vessels in superficial musculature. (A) Enlarged transverse section. (B) Enlarged partial view of C, with portions of the arterial walls cut away to show origin of arterioles and venules. (C) Enlarged lateral view of cutaneous vessels. (D) Posterior course of cutaneous vessels; no posterior commissure. From Godsil and Byers, 1944 (fig. 66).

mesenteric artery arises from the dorsal aorta beneath the third to fourth vertebra and forms two or three main branches that go to the liver, supply the vascular cones when present, and give off branches to the other visceral organs. The paired cutaneous arteries rise posterior to the origin of the coeliaco-mesenteric artery and course laterad almost or quite perpendicular to the aorta; they penetrate the lateral body musculature, and on each side form two branches beneath the skin that almost parallel one another to the caudal peduncle (fig. 20, 21). At about the level of the 30th vertebra, a posterior commissure may connect the dorsal and ventral branches of each side. Along their length, the lateral branches give off into their interspace arterioles, which are so dense that they seem to form a solid sheet penetrating the dark muscle (chiai).

Cutaneous veins accompany the arteries; the two parallel lateral branches join anteriorly on each side (fig. 22) to form a large vein that enters the duct of Cuvier, which in turn enters the sinus venosus.

If a post-cardinal vein is present it emerges from the first closed haemal arch, runs toward the right side in the kidney mass, and joins the right cutaneous vein. There is usually a cross-connection between the post-cardinal and left cutaneous veins.

Specific Characters

The coeliaco-mesenteric artery usually has two branches in *T. thynnus*, *T. maccoyii*, *T. alalunga*, and *T. atlanticus*, and three branches in *T. albacares* and *T. tonggol*. In *T. obesus* either two or three branches may be present in both Atlantic and Pacific specimens. Exceptions were noted in *T. albacares* and *T. atlanticus*.

A connecting branch near the liver between two of the coeliaco-mesenteric branches is present in *T. maccoyii*, may be present or absent in *T. thynnus*,

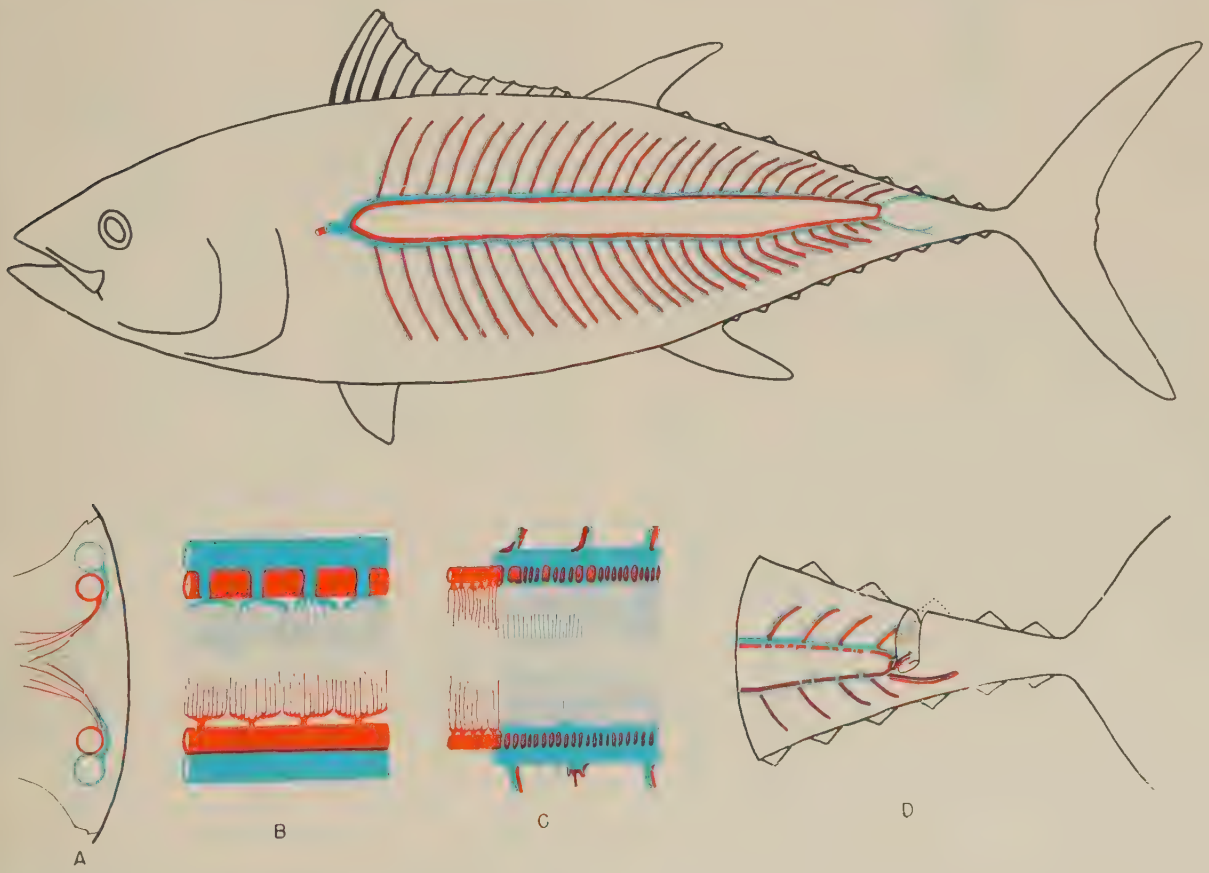


FIGURE 21.—Cutaneous system of arteries (red) and veins (blue) of *Thunnus albacares*. (upper) Course of cutaneous vessels in superficial musculature. (A) Enlarged transverse section. (B) Enlarged partial view of C, to show origin of venules (dorsal) and arterioles (ventral). (C) Enlarged lateral view of cutaneous vessels. (D) Posterior commissure. From Godsil and Byers, 1944 (fig. 31).

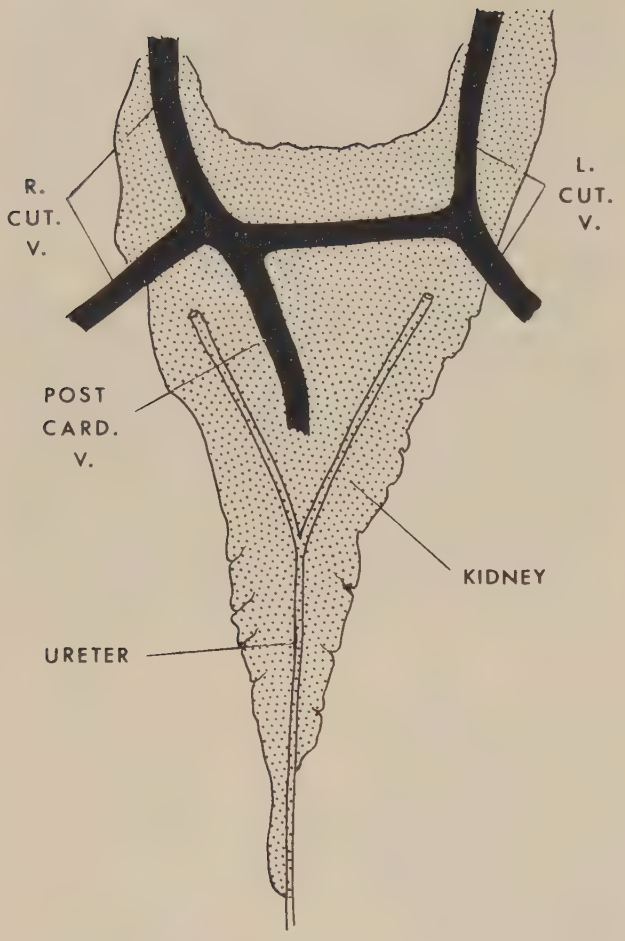


FIGURE 22.—Post-cardinal vein in relation to cutaneous veins and kidney in *Thunnus atlanticus*. Also typical of *T. obesus*, *T. albacares*, and *T. tonggol*.

T. obesus, and *T. albacares;* and appears to be absent in *T. alalunga*, *T. atlanticus*, and *T. tonggol*. Godsil and Byers (1944) implied that this connection is always, or nearly always, present in Pacific *T. albacares*. Godsil and Holmberg (1950) used its supposed absence in Atlantic *T. t. thynnus* as one character that differentiates Atlantic from Pacific specimens (*T. t. orientalis*), a conclusion which our observations do not support.

The cutaneous artery usually originates at the level of the third or fourth vertebra in *T. thynnus*, *T. maccoyii*, and *T. alalunga*, and at the sixth to eighth vertebra in *T. albacares*, *T. obesus*, *T. atlanticus*, and *T. tonggol*.

The cutaneous arteries pass laterally between the third and fourth ribs in all *T. thynnus*, *T. maccoyii*, and *T. alalunga* examined by us (also between the second and third according to Godsil and Holmberg, 1950); in *T. albacares*, *T. obesus*, *T. tonggol*, and *T. atlanticus* they pass between the fifth and sixth ribs, or occasionally between the fourth and fifth. Branching occurs between the fourth and fifth intermuscular bones in *T. thynnus*, *T. maccoyii*, and *T. alalunga*, and between the sixth and seventh in *T. albacares*, *T. obesus*, *T. tonggol*, and *T. atlanticus*. Godsil and Holmberg (1950) reported more *T. maccoyii* with branching between the fifth and sixth, and we observed this in one specimen of *T. t. thynnus*. In a significant number of our *T. albacares*, as well as two *T. obesus*, branching occurred between the seventh and eighth intermuscular bones.

A posterior commissure is present in *T. thynnus*, *T. maccoyii*, *T. albacares* (fig. 21), *T. tonggol*, and *T. atlanticus*, but absent in *T. alalunga*. In *T. obesus* it is present or absent (fig. 20). In all species except *T. albacares* and *T. maccoyii*, we encountered specimens in which we could not ascertain the presence of a commissure.

We noted the number and position of the rows of arterioles and venules arising from the lateral cutaneous vessels in relatively few specimens of each species (see fig. 23). *T. alalunga*, *T. albacares* (fig. 21), *T. atlanticus*, and *T. tonggol*, have one row from each vessel; in *T. alalunga* it originates on the mesial side, and in the other species on the lateral side. In *T. thynnus*, *T. maccoyii*, and *T. obesus* (fig. 20) two rows, one mesial and one lateral, arise from each vessel. Kishinouye (1923) reported two rows of venules and a single row of arterioles in Japanese *T. thynnus orientalis*. California specimens have two rows of arterioles (Godsil and Byers, 1944, and our observations). We feel certain that Kishinouye either was mistaken or relied on an unusual specimen.

In *T. albacares* large parallel trunks connect the posterior epibranchial and the cutaneous arteries on

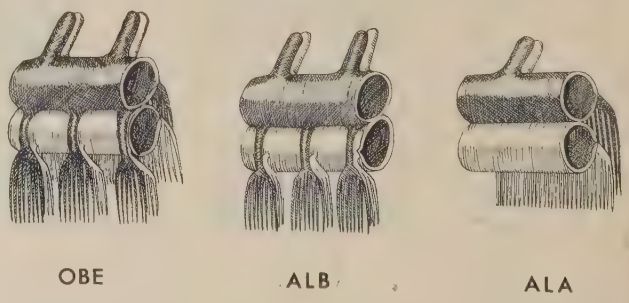


FIGURE 23.—Relationships of arterioles and venules to cutaneous artery (light) and vein (dark). Three patterns represented by *T. obesus* (OBE), *T. albacares* (ALB), and *T. alalunga* (ALA). Lateral view. After Kishinouye (1923).

each side; they are absent in the other species.

A post-cardinal vein joins the right cutaneous vein in *T. albacares*, *T. obesus*, *T. atlanticus*, and *T. tonggol;* it is absent in *T. thynnus*, *T. maccoyii*, and *T. alalunga*.

OLFACTORY ORGAN

As this manuscript was being completed, Iwai and Nakamura (1964b) described their use of the olfactory rosette to distinguish species of *Thunnus*. In each nasal cavity beneath the anterior naris is an olfactory rosette, consisting of numerous laminae arranged radially around a central axis. According to Iwai and Nakamura, *T. alalunga* is unique in having a pair of fleshy labia surrounding the short laminae. The laminae in *T. obesus* are described as smooth, greatly expanded distally with adipose tissue, and often partly fused distally. In *T. thynnus* the laminae in small specimens are smooth and of uniform thickness to the distal edge, whereas in larger specimens the laminae are smooth and distally expanded, but with little evident adipose tissue. *Thunnus maccoyii* is differentiated from *T. thynnus* by the presence, in some specimens, of slight fringing in the distal ends of the laminae. In *T. albacares* and *T. tonggol* the laminae are entirely fringed on their distal edges; and in large *T. albacares* the basal half of the rosette is densely spotted with pigment; however, Iwai and Nakamura admit that the rosettes of *T. tonggol* and small *T. albacares* resemble each other, and, from their figure 3, also resemble those of *T. maccoyii*. On the basis of admittedly insufficient material, Iwai, Nakamura, and Matsubara (1965) indicate that the nasal rosettes of *T. atlanticus* closely resemble those of *T. tonggol* except that the laminae of the former tend to have the distal ends folded inward.

We have examined very few nasal rosettes, but our observations indicate a need for more careful scrutiny of this character, with respect to normal variation and growth changes, before it is used widely. A specimen of *T. alalunga* and two of *T. obesus* agreed with Iwai and Nakamura (1964b), but in one *T. obesus* the laminae were lightly pigmented and had short, flat fimbriae along their entire length. Two specimens of *T. albacares* were distinctive in the abundance of pigment in the laminae, but while in one the fimbriae were very pronounced and finger-like, in the other they were less developed and flatter. Rosettes of one *T. atlanticus* and one *T. tonggol* were virtually identical and were similar to those of *T. albacares*, with dense, short, flat fimbriae on the laminae, but had less abundant pigment; folding of the distal ends of the laminae was not apparent in either species. In a larger specimen of *T. thynnus* from Cape Town, South Africa, the laminae were almost uniform in thickness to the distal edge and bore prominent flattened fimbriations along most of their length. These observations are enough at variance with those of Iwai and Nakamura that they clearly show the need for further study.

MERISTIC CHARACTERS

The species of *Thunnus* are essentially identical in the number of fin rays (table 1). The number of gill rakers is the only meristic character that we have found valuable in separating species of *Thunnus* (table 2).

Species Differences.—*T. atlanticus* has fewer gill rakers (19–25) than any other species of *Thunnus* in the Atlantic, and *T. tonggol* has fewer (19–26, rarely to 28) than any other *Thunnus* in the Indo-Pacific (table 2). *T. thynnus* and *T. maccoyii* have the greatest number of gill rakers in the genus (31–43). The other three species fall between these two groups with a combined range 23–35. The overlap between species with low, medium, and high numbers of gill rakers is very slight. The *T. thynnus-maccoyii* complex shows differences of some magni-

TABLE 1.—Range of variation in fin-ray counts in the species of *Thunnus*

[Based on original and published data]

Fin	Species					
	T. alalunga	*T. albacares*	*T. atlanticus*	*T. obesus*	*T. thynnus*	*T. tonggol*
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Dorsal spines	12–14	12–14	12–14	13–14	12–14	11–14
Second dorsal rays	13–16	13–16	12–15	14–16	13–15	14
Dorsal finlets	7–9	8–10	7–9	8–10	8–10	9
Total second dorsal rays	21–24	22–24	20–23	22–24	22–24	23
Anal rays	13–15	12–15	11–15	11–15	13–16	14
Anal finlets	7–9	7–10	6–8	7–10	7–9	8
Total anal rays	20–23	21–23	19–22	21–23	21–24	21–23
Pectoral rays	31–36	33–36	31–35	31–35	30–36	30–35

TABLE 2.—Total number of gill rakers on the first arch in the species of *Thunnus*

Number of rakers	*T. tonggol*			*T. atlanticus*	*T. obesus*			
	West Indian-Red Sea	SE Asia	Australia	West Atlantic	West Atlantic	East Atlantic	Central-West Pacific	East Pacific
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
19			3	1				
20		2	18	7				
21	1	2	43	29				
22		2	86	59				
23	4	4	54	21			1	
24	1	2	19	2			5	1
25	3		2	1	5	1	27	3
26	10				13	4	159	26
27	1				15	6	147	28
28	1				17	3	70	17
29					4	4	23	12
30						1	14	
31						1	2	
Number of fish	21	12	225	120	55	20	448	87
Average	25.1	21.7	22.0	21.9	27.3	27.6	26.9	27.1
Sources	6, 15, 17	6	6, 13, 25	2, 6, 12, 17	6, 12	6	3, 5, 30	5, 6, 8, 30

	T. alalunga					*T. albacares*				
	West Atlantic	East Atlantic	Indian Ocean	Central-West Pacific	East Pacific	West Atlantic	East Atlantic	West Indian Ocean	Central-West Pacific	East Pacific
25	1								1	
26	1	4	1	6	1		2	2	3	
27	10	18	5	45	6	6	3	7	24	2
28	20	55	9	142	21	11	11	22	73	8
29	15	50	15	176	26	33	51	54	194	20
30	6	27	11	96	8	37	88	58	242	50
31	2	4	1	15	2	30	126	23	202	51
32				1		9	80	5	93	24
33						1	23		21	6
34							7		2	
35							1			
Number of fish	55	158	42	481	64	127	392	171	855	161
Average	28.3	28.6	28.8	28.8	28.6	29.8	30.8	29.5	30.0	30.5
Sources	6, 12	6, 10, 11	14, 28, 29	5, 8, 29, 30	5, 8, 30	6, 12, 17	6, 11, 23	6, 19, 28	5, 8, 21, 22, 30	5, 8, 20, 30

	T. maccoyii		*T. t. orientalis*		*T. t. thynnus*	
	South Africa	Australia	Central-West Pacific	East Pacific	West Atlantic	East Atlantic-South Africa
31	1	10				
32	2	62		2		
33	3	84		2		
34	5	89		2	3	
35	1	54	3	14	2	4
36	1	25	6	10	12	8
37		6	2	11	32	40
38			1	2	63	88
39				2	102	105
40		1	1		40	74
41					29	36
42					4	7
43					1	4
Number of fish	13	331	13	45	288	366
Average	33.5	33.7	36.4	35.8	38.8	38.9
Sources	26	1, 5, 6, 9, 24	5, 6	6, 9, 12	6, 7, 9, 12	6, 18, 26, 27

Source:

1—Abe, 1955; 2—Beebe and Tee-Van, 1936; 3—Brock, 1949; 4—Crane, 1936; 5—Dung and Royce, 1953; 6—Gibbs and Collette, original data; 7—Ginsburg, 1953; 8—Godsil and Byers, 1944; 9—Godsil and Holmberg, 1950; 10—Letaconnoux, 1951; 11—Marchal, 1959; 12—Mather, 1964; 13—Munro, 1957; 14—Postel et al., 1960; 15—Ranade, 1961; 16—Rivas, 1954b; 17—Rivas, 1961; 18—Robins, 1957; 19—Royce, 1965; 20—Schaefer, 1948; 21—Schaefer, 1952; 22—Schaefer, 1955; 23—Schaefer and Walford, 1950; 24—Serventy, 1956a; 25—Serventy, 1956b; 26—Talbot, 1964; 27—Tiews, 1963; 28—Williams, 1964; 29—Yoshida and Otsu, 1963; 30—Japan Fishery Agency, 1964.

tude among populations in both the means (Atlantic 38.9, Pacific 35.9, *T. maccoyii* 33.7) and the modes (39, 35, 34). These differences and others can be used to separate the two subspecies, *T. thynnus thynnus* in the Atlantic and *T. thynnus orientalis* in the Pacific, and *T. maccoyii* in the southern Pacific

and Indian oceans. Populations of *T. tonggol* in the Red Sea and western Indian Ocean appear to have more gill rakers than those to the eastward.

MORPHOMETRIC CHARACTERS

Relative lengths of body parts have limited value in species identification of tunas, although they have been widely used by many investigators. Allometric growth has been demonstrated for many, if not most, body parts and has been responsible for many misconceptions. A classic example of allometry involves the dorsal and anal fins of *T. albacares* which become relatively much longer in large specimens. Furthermore, the length attained by these fins varies geographically in a complex fashion (Royce, 1965). Lack of consideration of these factors has resulted in the description of numerous nominal species. Many limited analyses have shown statistically significant differences between populations of widely distributed species (cf. Kurogane and Hiyama, 1957b, 1958a, 1959 for *T. alalunga*).

Of the many measurements that can be made, only the following appear to be of importance in distinguishing tuna species: dorsal and anal fin heights, pectoral fin length, placement of second dorsal fin, greatest body depth, and diameter of eye (or orbit).

Our conclusions are based, as often as possible, on data from many parts of the range of each species. Where these data have shown no noteworthy geographic differences, we consider them together as a single unit. Otherwise, the differences are mentioned. In addition to our original data, we have leaned heavily upon Dung and Royce (1953) for raw data, and have used many other sources. Our information has significant gaps that can be filled only by future work or by use of unpublished data from other workers. All species are more or less deficient in morphometric data for specimens below 400 mm. For the Atlantic, such data are few or lacking for *T. alalunga* less than 900 mm.; for *T. atlanticus* larger than 650 mm.; and for *T. obesus* less than 1,000 mm. For the Pacific and Indian Oceans, *T. maccoyii* is represented by data on only four specimens outside the 650–750 mm. range, and our sparse Indian Ocean data for all species are almost entirely from specimens sent to us as a result of cruises of the R/V *Anton Bruun* during the International Indian Ocean Expedition. Our interpretations must be judged with these deficiencies in mind.

Heights of the second dorsal and anal fins have received much attention, especially in *T. albacares*, in which the positive allometry of both these fins relative to fork length, apparently characteristic of all species, is most pronounced. This allometry has led to the description of long-finned nominal species in both the Atlantic and Pacific and even to the establishment of a new genus (*Semathunnus*). The species are compared in figs. 24 and 25, in which the large *T. albacares* are western Atlantic specimens. The few data for *T. maccoyii* fall in the range of *T. thynnus* and are not discussed separately.

As many workers have shown and as Royce (1965) has most recently demonstrated, different popula-

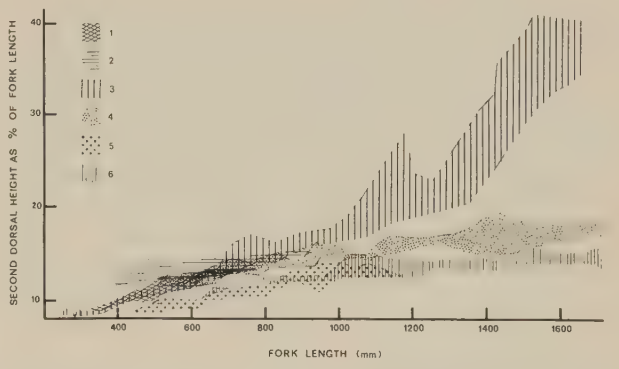


FIGURE 24.—Relative height of second dorsal fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

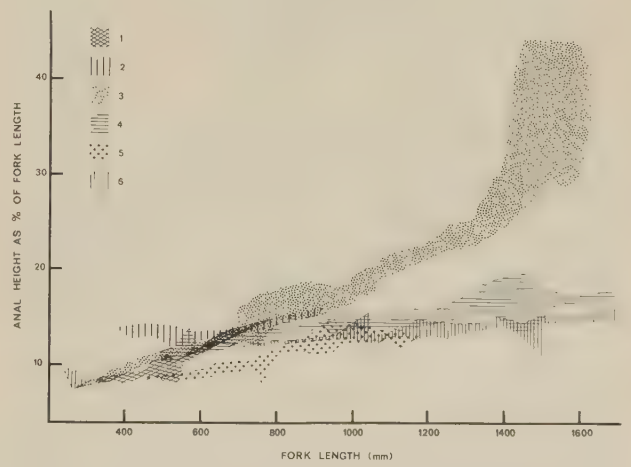


FIGURE 25.—Relative height of anal fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

tions of *T. albacares* show different regressions, but in adults of this species the fins always become higher than in any other species of *Thunnus*. In the equatorial Pacific the fin heights vary in clinal fashion from highest in the west to lowest in the east. Western Atlantic specimens have very high fins, thereby resembling those from the western equatorial Pacific; eastern Atlantic (Angola) specimens have lower fins, as do those from the eastern Pacific.

At sizes between 350 and 600 mm., *T. tonggol* appears to have higher fins than any other species of *Thunnus*. From about 500 to 800 mm., *T. alalunga* has the lowest fins. The other five species are difficult to distinguish until about 700 mm. Beyond 800 mm., *T. albacares* clearly develops the highest fins, *T. thynnus* and *T. alalunga* remain the shortest, and *T. obesus* and *T. tonggol* are intermediate.

The pectoral fin shows a growth pattern that is probably similar in all species, but which differs among the species in size of fin and fork length at times of inflection. Simply stated, the pectoral fin undergoes a period or stanza of increase in length relative to fork length in juveniles, followed by an isometric period that leads into a final and continuous stanza of relative decrease in length (fig. 26). Size range of the stanzas is shown in table 3 for each adequately represented species. The smallest *T. tonggol* for which data were available are probably in the size range at which the distinction between increasing relative fin size and isometry is difficult to distinguish; hence the stanzas could not be determined.

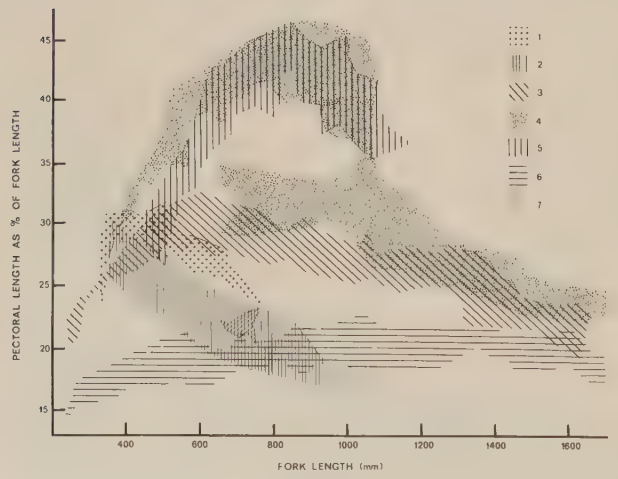


FIGURE 26.—Relative length of pectoral fin in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 12, 21, 27, 28, 42, 45–50), Godsil and Holmberg (1950: 54–55), and Serventy (1956b). 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus;* 7—*T. maccoyii.*

TABLE 3.—*Approximate range in fork length of growth stanzas of pectoral fins in species of* Thunnus. *Smallest size limited by available data*

Species	Increase	Isometric	Decrease
	Millimeters	*Millimeters*	*Millimeters*
alalunga	450–700	700–900	900 +
obesus (Indo-Pacific)	350–700	700–900	900 +
obesus (Atlantic)	?	?650–1,000	1,000 +
albacares	250–500	500–650	650 +
atlanticus	? –350	350–500	500 +
tonggol	?	?	?400 +
thynnus	150–850	850–1,600	1,600 +
maccoyii	?	?650–1,450	?

At less than 500 mm., only *T. thynnus* is distinct, with pectorals 21 percent of fork length or less. Data for *T. maccoyii* are lacking. All other species overlap more or less in the 25–31 percent range, although between 400 and 500 mm. species distinctions begin to be apparent (viz. Pacific *T. obesus* pectorals become relatively longer, those of *T. tonggol* shorter).

The marked positively allometric growth of the pectorals of *T. alalunga* and Pacific *T. obesus* makes these two forms clearly distinctive from all others between 500 and 1,200 mm. (fig. 26). Most specimens have fins 34–46 percent of fork length. Up to 700 mm., *T. alalunga* has slightly shorter fins than Pacific *T. obesus*, but from 700–1,200 mm. they are virtually identical. Atlantic *T. obesus* in the 650–1,200 mm. range (no data were available for smaller specimens) appear to have significantly shorter pectorals than Pacific specimens: 29–35 percent at sizes of 650–1,000 mm., then gradually decreasing until no suggestion of difference is seen above 1,300 mm.

In *T. albacares* a gradual negative allometry after 600 mm. keeps the pectorals shorter than in *T. alalunga* or either Atlantic or Pacific *T. obesus* until about 1,100 mm., when overlap with *T. obesus* begins to increase.

Whereas the pectorals of *T. atlanticus* are, at first, very similar in length to those of *T. albacares*, the more rapid decline in relative length makes them at sizes above 600 mm. even shorter than in *T. albacares*.

The greatest negative allometry is seen in T. *tonggol*, which, at 500 mm., already shows the trend that brings the pectoral length into the ranges of *T. maccoyii* and *T. thynnus* between 650 and 900 mm. The fins are the shortest of all the species at fork

lengths from 900 to 1,050 mm. (the maximum size of *T. tonggol* for which data were available).

Except for the size range where *T. tonggol* overlaps it, *T. thynnus* has pectorals consistently shorter than those of other species, the longest on record being about 23 percent of fork length.

Although more data are needed for *T. maccoyii*, it appears that this species has a slightly longer pectoral fin than *T. thynnus*. From 650–750 mm. fork length, for which a fair amount of data is available, the fin of *T. maccoyii* is 20–24 percent of fork length, that of *T. thynnus* 17–21 percent. A few specimens of *T. maccoyii* between 900 and 1,000 mm., and one of 1,445 mm. have pectorals 22–23 percent of fork length, also slightly longer than those of similar sized *T. thynnus*. The ranges given by Iwai, Nakamura, and Matsubara (1965: 31, 33) of 4.8–6.0 in fork length (=16.7–21.7 percent) for *T. thynnus* and 4.4–4.5 in fork length (=22.2–22.7 percent) for *T. maccoyii* suggest a distinctness of separation that is not upheld by our data, although the basic species differences in pectoral length appear to be real.

The distance from snout to second dorsal origin relative to fork length (fig. 27) shows a negative regression in all species of *Thunnus* over 400 mm. When size is taken into account, this measurement provides a reliable separation of some species, but a simple statement of range is inadequate. For example, *T. tonggol* appears distinct throughout its size range (maximum around 1,000 mm.) but larger *T. albacares*, *T. obesus*, and *T. thynnus* all have a distance that is the same as that of smaller *T. tonggol*.

Throughout the size ranges examined by us (fig. 27) the distance is greatest in *T. alalunga* and least in

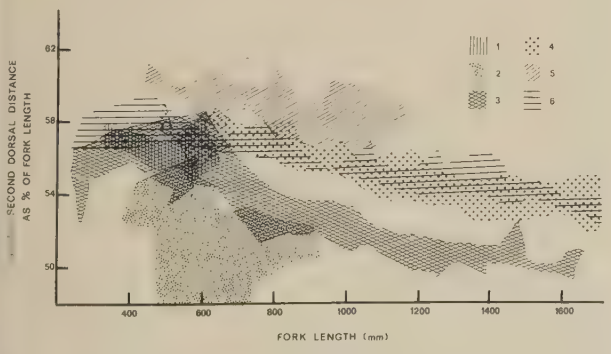


FIGURE 27.—Relative distance from snout to second dorsal origin in *Thunnus* species. Data, in additon to our own, include Dung and Royce (1953: tables 12, 21, 28, 42, 50–54). 1—*T. atlanticus*; 2—*T. tonggol*; 3—*T. albacares*; 4—*T. obesus*; 5—*T. alalunga*; 6—*T. thynnus*.

T. tonggol. Two intermediate groups can be categorized: one with a shorter distance that includes *T. atlanticus* and *T. albacares*, and one with a longer distance that includes *T. obesus* and *T. thynnus*. The meager data for *T. maccoyii* fall in the range of *T. thynnus*. Below a fork length of about 600 mm. there is so much overlap that the usefulness of snout-second dorsal distance in species distinction is doubtful, but above 600 mm. it appears to be useful.

Greatest body depth is shown in fig. 28. This

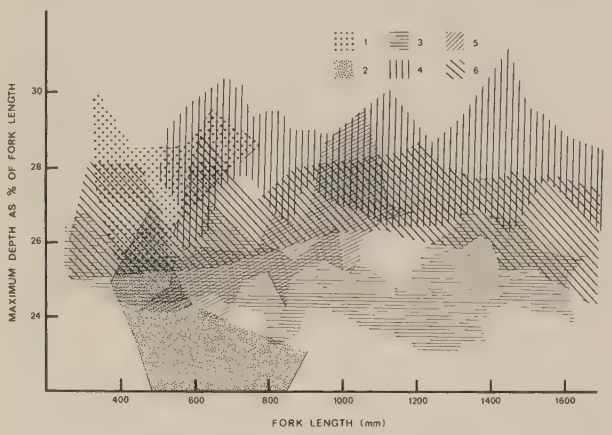


FIGURE 28.—Relative greatest body depth in *Thunnus* species. Data, in addition to our own, include Dung and Royce (1953: tables 27, 28, 42). 1—*T. atlanticus*; 2—T. *tonggol*; 3—*T. albacares*; 4—*T. obesus*; 5—*T. alalunga*; 6—*T. thynnus*.

character is so variable that it should not be used by itself. Rather, there are tendencies which, with other characters, can be helpful in species determination.

In specimens less than about 600 mm. fork length, overlap is particularly evident, but two categories can be based on greatest depth: deep-bodied species, including *T. obesus*, *T. thynnus*, and *T. atlanticus*, with depths usually 26–30 percent of fork length; and slender species, including *T. albacares*, *T. tonggol*, and *T. alalunga*, with depths usually 23–26 percent of fork length. The few data for *T. maccoyii* fall in with *T. thynnus*.

There appears to be little change in depth relative to fork length from 600 to 1,500 mm. in any species except *T. alalunga*, in which the relative depth increases gradually until specimens over 1,000 mm. are clearly in the deep-bodied category.

The two species that commonly become larger than 1,500 mm., *T. obesus* and *T. thynnus*, exhibit

increased variability at these larger sizes. In *T. thynnus* this is particularly evident; specimens over 2,000 mm. fork length (not shown in fig. 28) appear randomly distributed over a range of body depths from 22–29 percent of fork length, which is almost the entire range of all species combined.

The greatest body depth is found in individuals of *T. obesus* at all sizes over 600 mm., but the species overlaps with *T. atlanticus*, *T. thynnus*, or *T. alalunga* throughout its known size range.

Eye size, in combination with other characters, is a useful species criterion, but the negative allometry must be considered. Because we measured the bony orbit, our data are not comparable with most other published data. We recommend that future workers use iris diameter.

Fig. 29 compares the species. Both *T. alalunga* and *T. atlanticus* exhibit wide variation in eye diameter, making categorical statements difficult. At less than 600 mm. fork length the smallest orbit diameter is found in *T. thynnus* and *T. tonggol*, the largest in *T. atlanticus* and *T. alalunga*, and intermediate in *T. albacares; T. obesus* is not represented.

At sizes greater than 600 mm., *T. obesus* clearly has the largest orbit diameter. Variation in *T. alalunga* covers the range from largest to smallest. The other species have so much overlap with one another that species distinctions are impossible.

COLORATION

Colors and color patterns of tunas have limited use in tuna systematics because they show great individual and age variation, and because they may be lost after death and preservation. Nevertheless, there are some excellent color characters, in spite of the difficulty in verbal expression of many of them. Many of the descriptions are taken from Mather (1964).

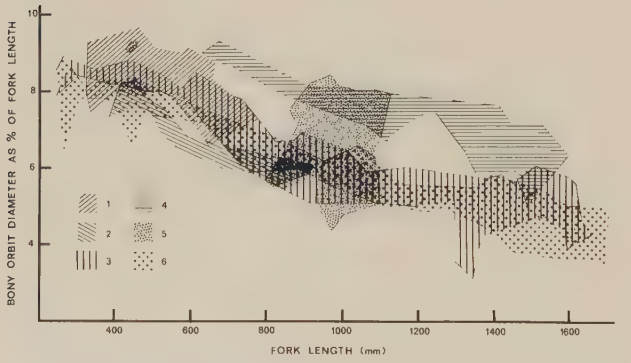


FIGURE 29.—Diameter of bony orbit relative to fork length in *Thunnus* species. Only our data used. 1—*T. atlanticus;* 2—*T. tonggol;* 3—*T. albacares;* 4—*T. obesus;* 5—*T. alalunga;* 6—*T. thynnus.*

Body. Most *Thunnus* species are iridescent dark blue above and silvery below. *T. albacares* is the most brilliantly colored, with a shining golden lateral band. *T. atlanticus* also has a prominent gold lateral band, but its body is usually very dark compared with other species. *T. obesus* may display a trace of a gold band, but the band is apparently absent in *T. thynnus* and *T. tonggol* and is replaced by an iridescent blue band in *T. alalunga.*

Small specimens of all species may display a pattern of white spots or streaks ventrolaterally. In *T. tonggol* these markings consist of horizontally elongated spots. The other six species have rounded spots that are either randomly distributed or tend to become arranged in vertical rows that alternate with vertical white lines; horizontally elongated spots are sometimes seen on the caudal peduncle but rarely farther anteriorly. This pattern is usually lost in large individuals, although it may be retained in specimens of *T. albacares* and *T. thynnus* up to 1,500–1,600 mm.

In *T. maccoyii*, alone among the species of *Thunnus*, the caudal keels are an unmistakable bright yellow. In the fish markets of Japan, we were able to recognize *T. maccoyii* from a considerable distance on the basis of this character. However, we suspect the keels may lose their yellow in larger adults.

Fins. The color of the first dorsal fin is variable. It may be entirely white, or there may be a yellow suffusion, and the distal margin may be black. Too few observations have been made to enable us to characterize the species. The second dorsal and anal fins usually have yellow tips in all but *T. alalunga* and *T. atlanticus*, which have dark fins with white distal margins. The dorsal and anal finlets are usually bright yellow with black margins in all except *T. alalunga* and *T. atlanticus.* In *T. albacares* the black margin is usually very narrow, while in *T. obesus* it is wider. *T. alalunga* may have yellow in the dorsal and some anal finlets, but the anal finlets are commonly all silvery or dusky. Both the dorsal and anal finlets of *T. atlanticus* are almost invariably dusky with white margins; yellow has been observed in these finlets only in frozen specimens. June (1952b) reported black dorsal and anal finlets in an unusual specimen of *T. albacares* from the central Pacific.

The caudal fin of *T. alalunga* has a narrow, white trailing margin that distinguishes it from all other *Thunnus*, in which the white margin is lacking.

Specific Characters. The uniformly white-margined dusky finlets of *T. atlanticus*, the white caudal margin of *T. alalunga*, the horizontally elongated ventrolateral spots of *T. tonggol*, and the yellow caudal keels of *T. maccoyii* are the only color characters we regard as generally useful in distinguishing species, and confusing examples of other species with these same characters have been observed.

PART 2. SYSTEMATICS

Workers have differed in their interpretations of the suprageneric relationship of tunas and the mackerel-like fishes. Regan (1909) and Starks (1910) placed all of these fishes in the single family Scombridae. Kishinouye (1915, 1917, 1923) recognized four families: Scombridae, Cybiidae, Katsuwonidae, and Thunnidae, the last two of which he (1917, 1923) recognized as an order Plecostei, separate from the Teleostei, in which he included all other higher bony fishes. Takahashi (1924, 1926) disagreed with the recognition of a distinct order but did not alter the four families. More recently, Fraser-Brunner (1950) placed the tuna-like and mackerel-like fishes back in the Scombridae. Berg (1940, 1955) is one of the few recent taxonomists who followed Kishinouye in placing the tunas in a separate order Thunniformes. For reasons outlined elsewhere (Collette and Gibbs, 1963), we follow Regan, Starks, and Fraser-Brunner in placing all of the tunas and other mackerel-like fishes in the family Scombridae.

It is possible to divide the Scombridae into smaller units. *Gasterochisma* is so different from the other scombrids that it deserves at least subfamily status. Fraser-Brunner (1950) recognized only the subfamilies Gasterochismatinae and Scombrinae. Nakamura (1965) considered *Thunnus* and *Euthynnus* (including *Katsuwonus*) as a third subfamily, Thunninae. In the comparative diagnosis of the genus *Thunnus* which follows, we give suggestions of other possible subdivisions. Until a thorough anatomical study is completed, however, we do not wish to present formally a revised family classification.

THUNNUS SOUTH, 1845

Thynnus Cuvier, 1817: 313 (type-species: *Scomber thynnus* Linnaeus, 1758, by absolute tautonymy; preoccupied by *Thynnus* Fabricius, 1775, a genus of Hymenoptera).

Orcynus Cuvier, 1817: 314 (type-species: *Scomber germo* Lacépède, 1800 [= *Scomber alalunga* Bonnaterre, 1788], by subsequent designation of Jordan, 1888: 180; preoccupied by *Orcynus* Rafinesque, 1815, a substitute for *Scomberoides* Lacépède).

Thinnus S. D. W., 1837 (emendation of *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758; suppression in favor of *Thunnus* South, 1845 requested by Collette and Gibbs, 1964).

Thunnus South, 1845 (emendation of *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758).

Orycnus Cooper, 1863: 77 (substitute name for *Thynnus* Cuvier, 1817, and therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758; not *Orycnus* of Gill, 1861, a misprint for *Orcynus* Cuvier, 1817).

Albacora Jordan, 1888: 180 (substitute name for *Thynnus* Cuvier, 1817, therefore taking the same type-species: *Scomber thynnus* Linnaeus, 1758).

Germo Jordan, 1888: 180 (substitute name for *Orcynus* Cuvier, 1817, therefore taking the same type-species: *Scomber germo* Lacépède, 1800 [= *Scomber alalunga* Bonnaterre, 1788]).

Parathunnus Kishinouye, 1923: 442 (type-species: *Thunnus mebachi* Kishinouye, 1923 [= *Thynnus obesus* Lowe, 1839], by monotypy).

Neothunnus Kishinouye, 1923: 445 (type-species: *Thynnus macropterus* Temminck and Schlegel, 1844 [= *Scomber albacares* Bonnaterre, 1788] by subsequent designation of Jordan and Hubbs, 1925: 218).

Kishinoella Jordan and Hubbs, 1925: 219 (type-species: *Thunnus rarus* Kishinouye, 1923 [= *Thynnus tonggol* Bleeker, 1851] by original designation).

Semathunnus Fowler, 1933: 163 (type-species: *Semathunnus guildi* Fowler, 1933 [= *Scomber albacares* Bonnaterre, 1788] by original designation).

Comparative Diagnosis

The tunas, genus *Thunnus*, comprise a group of seven closely related species representing the most advanced members of the family Scombridae

(sensu Regan, 1909; Starks, 1910; and Fraser-Brunner, 1950). The subfamily Scombrinae of Fraser-Brunner, which includes all Scombridae except *Gasterochisma*, is divisible into two major groups (Collette and Gibbs, 1963). The more primitive *Scomber*, *Rastrelliger*, *Scomberomorus*, *Grammatorcynus*, and *Acanthocybium* have a posterior notch in the hypural plate and lack a bony lateral keel on the caudal vertebrae. The more advanced group, consisting of *Gymnosarda*, *Orcynopsis*, *Sarda*, *Cybiosarda*, *Auxis*, *Euthynnus*, *Katsuwonus*, *Allothunnus*, and *Thunnus*, lack a hypural notch and have a bony caudal keel. Within the latter group another category may be recognized as including *Allothunnus*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* (the Plecostei of Kishinouye, 1917, 1923), characterized by the presence of well-developed prootic pits and (except *Allothunnus*) a subcutaneous vascular system. Within this group of higher scombrids, the genus *Thunnus* is characterized by the presence of fronto-parietal foramina, a particularly well-developed subcutaneous vascular system with two long lateral branches on each side, and the body fully covered with scales. *Auxis* and *Allothunnus* lack fronto-parietal foramina. *Auxis*, *Euthynnus*, and *Katsuwonus* have the body squamation limited to an anterior corselet and do not have the subcutaneous vascular system as well-developed as in *Thunnus;* the lower lateral branch is either short, or, if long as in *K. pelamis*, it meets the upper branch mesial to the ribs.

Validity of Nominal Genera

Cuvier (1817: 312–314) was the first to divide the large Linnaean genus *Scomber*. For the tunas he proposed *Thynnus* for *T. thynnus* and *Orcynus* for *T. alalunga*. Later (in Cuvier and Valenciennes, 1831) he placed his subgenus *Orcynus* in the synonymy of *Thynnus*. Several subsequent workers independently realized that *Thynnus* Cuvier was preoccupied by *Thynnus* Fabricius in insects. Thus Cooper (1863) accepted Gill's (1861) *Orycnus*, a misspelling of *Orcynus*, as a replacement name for *Thynnus* Cuvier (see also Gill, 1889). Jordan (1888) overlooked this action and proposed *Albacora* to replace *Thynnus*, and *Germo* to replace *Orcynus*. Gill (1894) settled matters by showing that South (1845) had previously suggested *Thunnus* to replace *Thynnus* Cuvier. Most subsequent workers have used *Thunnus* South either for *T. thynnus* alone or for several or all of the seven species we refer to *Thunnus*. Whitley (1955) recently discovered an earlier modification of *Thynnus* Cuvier, namely *Thinnus* S.D.W., 1837. S.D.W. (perhaps S. D. Wood, according to Whitley) emended a number of names by changing y to i, ph to f, ... As far as we can determine, only Abe (1955) followed Whitley in the usage of *Thinnus* S. D. W. In order to stabilize the consistent usage of *Thunnus* South from about 1890 to the present, we have applied to the International Commission of Zoological Nomenclature to suppress *Thinnus* S. D. W. (Collette and Gibbs, 1964).

Other nominal genera have been proposed, based on anatomical data. Kishinouye (1923) described two additional genera: *Parathunnus* based on *T. obesus* (as *mebachi*) and *Neothunnus* which included *albacares* (as *macropterus*) and *tonggol* (as *rarus*). He based this division on anatomical characters such as liver striations, the level at which the subcutaneous blood vessels pass through the myomere, and presence or absence of the postcardinal vein. Jordan and Hubbs (1925) then proposed *Kishinoella* for *T. tonggol* (as *rarus*), the only tuna that generally lacks a swim bladder. We have summarized these differences and others that have been used to distinguish genera or subgenera (table 4). A large number of different arrangements can be made depending on which characters one wishes to emphasize as "basic." *Thunnus* can be divided into two groups using the area of origin of the cutaneous artery, the level at which it passes between the ribs, and the intermuscular bones between which it divides: *T. alalunga*, *T. maccoyii*, and *T. thynnus* in one and *T. obesus*, *T. albacares*, *T. tonggol*, and *T. atlanticus* in the other. On the basis of number of arteriolar rows, *T. thynnus*, *T. maccoyii*, and *T. obesus* stand out from the other species. The presence of liver striations and vascular cones and the length of the liver lobes place *T. alalunga*, *T. maccoyii*, *T. thynnus*, and *T. obesus* in one group, the remaining three species in another. The absence of a swimbladder distinguishes *T. tonggol* from the other species, but the swimbladder may be rudimentary in *T. maccoyii*, and a swimbladder has been observed in small *T. tonggol*. *T. atlanticus* is unique in *Thunnus* in having 19 instead of 18 precaudal vertebrae. *T. atlanticus* and *T. tonggol* fall together on the basis of their low number of gill rakers, and *T. thynnus* stands out with the highest number in the genus. *T. alalunga* is unique in the position of spleen and stomach, in the shape of the first ventrally directed parapophysis,

TABLE 4.—*Comparison of diagnostic characters of the species of* Thunnus

Character	*T. alalunga*	*T. thynnus*	*T. maccoyii*	*T. obesus*	*T. albacares*	*T. atlanticus*	*T. tonggol*
Cutaneous artery orginates at vertebra number	3–4	3–4	3–4	6–8	6–8	6–8	6–8
Cutaneous artery passes between ribs number	3–4	3–4	3–4, 2–3	5–6	5–6	5–6	5–6
Cutaneous artery divides between intermuscular bones number	4–5	4–5	4–5, 3–4	6–7	6–7	6–7	6–7
Number of arteriolar rows from cutaneous artery	1	2	2	2	1	1	1
Post-cardinal vein	absent	absent	absent	present	present	present	present
Liver striations and vascular cones	present	present	present	present	absent	absent	absent
Liver lobes	subequal	subequal	subequal	subequal	right long	right long	right long
Swimbladder	present	present	present	present	present	present	absent or rudimentary
Spleen position	right	left	left	left	left	left	left
First haemal arch on vertebra number	10	10(11)	10	11(10)	11(10, 12)	11(10)	11(12)
First ventrally directed parapophysis on vertebra	9	8	9	9	9	9	10
Anterior haemal prezygapophysis position	on centrum	near centrum	near centrum	near centrum	well ventrad	well ventrad	well ventrad
Anterior haemal postzygapophysis length	short	short	short	short	long	long	long
Ventrolateral foramina size	small	small	small	small	large	large	large
Number of precaudal vertebrae	18	18	18	18	18	19	18
Posterior parasphenoid margin	angulate	angulate	angulate	angulate	non-angulate	non-angulate	non-angulate
Pectoral length	long	short	short	long to medium	medium	medium	medium to short
Gill raker number	25–31	34–43	31–40	23–31	26–34	19–25	19–28

and in the flattened haemal spine of its first caudal vertebra.

Not only is the subdivision of *Thunnus* into genera or subgenera an arbitrary matter, but such subdivision obscures the close relationship among the species. In this concept we agree with such workers as Rivas (1951, but not 1961), de Sylva (1955), and Iwai, Nakamura, and Matsubara (1965). *Thunnus* can be divided into as many as six groups, but these are essentially species, not subgenera or genera (table 4). However, based on the 18 characters in table 4 (excluding pectoral fin length), there do appear to be two groups of species. *T. alalunga*, *T. thynnus*, and *T. maccoyii* are similar to each other in 14-16 characters; *T. albacares*, *T. atlanticus*, and *T. tonggol* are similar to each other in 15-16 characters; and *T. obesus* is in between the two groups, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares*. This agrees with the intra-generic relationships presented by Iwai et al. (1965) and Nakamura (1965). It disagrees with Watson's (1964) groups where she placed *T. obesus* in the first group. *T. obesus* is similar to the first group in several liver and vertebral characters but fits with the second group in position of the cutaneous artery, presence of the post-cardinal vein, and position of the first haemal arch.

The synonymy of each species includes all the combinations of names we have found, together with selected references containing information on anatomy, morphometry, and distribution. Readers wishing more references should consult tuna bibliographies such as Corwin (1930), Shimada (1951), and volume 4 of the "Proceedings of the World Scinetific Meeting on the Biology of the Tunas and Related Species" (Bernabei, 1964).

THUNNUS ALALUNGA (Bonnaterre, 1788) ALBACORE

Scomber pinnis pectoralibus longissimis Cetti, 1777: 191-193 (Sardinia, *alalunga* in vernacular).

Scomber alalunga Bonnaterre, 1788: 139 (original description based on Cetti). Walbaum, 1792: 222. Risso, 1810: 169-170.

Scomber alatunga Gmelin, 1789: 1330 (original description based on Cetti; "*alatunga*" a misprint for "*alalunga*"; date of publication according to Cat. Books British Mus. is 1789, not 1788). Lacépède, 1800: 599 and 1802: 21–22.

Scomber germo Lacépède, 1800: 598 (original description in table of species of *Scomber;* misspelled *S. germon*). Lacépède, 1802: 1–8 (description: S. Pacific Ocean, 17° S., 103° W.; based on Commerson's manuscript).

Orcynus germon, Cuvier, 1817: 314.

Orcynus alalonga, Risso, 1826: 419–420 (Mediterranean).

Thynnus alalonga, Cuvier *in* Cuvier and Valenciennes, 1831: 87–95 (Atlantic), fig. 215. Lowe, 1839: 78 and 1849: 2 (Madeira). Günther, 1860: 366. Cunningham, 1910: 109–110 (synonymy, description; St. Helena), fig. 3.

Thynnus pacificus Cuvier *in* Cuvier and Valenciennes, 1831: 96–97 (substitute name for *Scomber germo* Lacépède, 1800).

Thunnus alalonga, South, 1845: 622.

Thunnus pacificus, South, 1845: 622.

Orcynus pacificus (not of Cuvier) Cooper, 1863: 75–77 (original description; California), fig. 19.

Orcynus germo, Lütken, 1880: 468–472, 596 (synonymy in part), pl. 3, figs. 1–2 (young). Kitahara, 1897: 2 (description; Japan), pl. 2, fig. 3.

Germo alalonga, Jordan, 1888: 180. Barnard, 1927: 799 (S. Africa). Morice, 1953: 68-69, fig. 3 (description of liver; E. Atlantic).

Albacora alalonga, Dresslar and Fesler, 1889: 438–439 (synonymy in part), pl. 6.

Germo alalunga, Jordan and Evermann, 1896: 871 (description; synonymy in part; Atlantic and Pacific). Jordan and Jordan, 1922: 33 (Hawaii). Meek and Hildebrand, 1923: 316–317 (description; synonymy in part). Jordan and Evermann, 1926: 15 (Atlantic). Buen, 1930: 48 (synonymy in part), fig. 6. Jordan, Evermann, and Clark, 1930: 260 (synonymy in part). Fowler, 1936: 621–623 (synonymy in part; description), fig. 280. Walford, 1937: 14–17 (description; a single worldwide species of albacore), color pl. 35. Fowler, 1944: 498 (W. of Chile). Tinker, 1944: 158–159 (Hawaii), pl. 1, fig. 6. Brock, 1949: 267 (in key to Hawaiian tunas). Le Gall, 1949 (synonymy, description, biology). Smith, 1949, 1953: 299 (S. Africa), pl. 66, fig. 835. Fernandez-Yepez and Santaella, 1956: 12, fig. 3, pls. 1, 5, (Venezuela). Tucker, 1955 (British Seas). Otsu, 1960 (migration, growth; N. Pacific). Frade and Vilela, 1962: 17–59 (morphology, biology; E. Atlantic). Postel, 1963 (description, biology; E. Atlantic).

Thynnus alalunga, Clarke, 1900 (Scotland).

Germo germon, Fowler, 1905: 761–763 (Sumatra).

Germo germo, Jordan and Seale, 1906: 228 (Samoa). Jordan and Hubbs, 1925: 217 (Japan). Jordan and Evermann, 1926: 16 (Pacific), pl. 3, fig. 1. Jordan et al., 1930: 260 (synonymy).

Thunnus alalunga, Jordan, Tanaka, and Snyder, 1913: 120 (Japan). Kishinouye, 1915: 18 (description; Japan). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 143 (synonymy in part; distribution), fig. 5. Rivas, 1951: 222–223 (synonymy, description; Atlantic). de Sylva, 1955: 33 (relationships, osteology), fig. 56 (neurocranium). Bullis and Mather, 1956 (counts, measurements; key to Caribbean *Thunnus*), fig. 3. Kurogane and Hiyama, 1957b (morphometry; NW. Pacific). Gosline and Brock, 1960: 259–260 (description; Hawaii), 336–337 (synonymy), fig. 257i. Mather and Gibbs, 1957: 242–243 (39° 45′ N., 73° 00′ W.). Jones and Silas, 1960: 382–383 (Indian Ocean), fig. 9. Talbot and Penrith, 1962: 558 (S. Africa). Jones and Silas, 1963: 1790–1791 (Indian Ocean). Rodrigues Lima and Wise, 1963 (distribution; W. tropical Atlantic). Squire, 1963 (distribution; NW. Atlantic). Talbot and Penrith, 1963: 609–616 (description, biology; S. Africa). Iwai and Nakamura, 1964: 6, fig. 3a (olfactory rosettes). Williams, 1964: 121 (E. Africa). Iwai et al., 1965: 3–5 (synonymy), 28–30 (description), figs. 13, 14, 15. Nakamura, 1965: 13–17, figs. 1, 2, 3A, 4, 5A (osteology). Merritt and Thorp, 1966: 377 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus germo, Kishinouye, 1923: 434 (anatomy; Japan), figs. 20, 46, 52. Serventy, 1941: 23–24 (Australia), pl. 2. Godsil and Byers, 1944: 70–87 (anatomy; comparison of Pacific specimens), figs. 36–47. Godsil, 1948 (morphometric comparison of Japanese, Hawaiian, and American specimens). Alverson, 1961 (distribution; NE. Pacific). Clemens, 1961 (migration, age, growth; N. Pacific). Clemens, 1963 (migration; N. Pacific). Yoshida and Otsu, 1963 (biology; Pacific and Indian oceans). Otsu and Uchida, 1963 (migration; Pacific). Jones and Silas, 1964: 34–36 (Indian Ocean).

Germo germon steadi Whitley, 1933: 81–83 (original description; New South Wales), pl. 11, fig. 1.

Thunnus germon, Tortonese, 1939: 324–325 (W. coast S. America).

Thunnus alalunga germo, Munro, 1958: 111 (Australia).

Types of Nominal Species

Scomber alalunga Bonnaterre, 1788. No type specimens. Original description based on Cetti, 1777 (*Scomber pinnis pectoralibus longissimus*).

Scomber alalunga Gmelin, 1789. No type specimens. Original description based on Cetti, 1777. Specific name, published as *alatunga*, a misprint.

Scomber germo Lacépède, 1800. No type specimens. Original description based on manuscript by Commerson. Specific name spelled *germon* in table of species of *Scomber* (1800), spelled *germo* in description (1802).

Thynnus pacificus Cuvier, *in* Cuvier and Valenciennes, 1831. No type specimens. Original description based on Lacépède's *Scomber germo* (1800) and on Commerson's manuscript. The specimen,

MNHN A. 6862, considered as the holotype by Bauchot and Blanc (1961, p. 377) and Blanc and Bauchot (1964, p. 456) is, therefore, not a type (Collette, 1966).

Orcynus pacificus Cooper, 1863. No type specimen, although mention is made of "State collection, species 1033."

Germo germon steadi Whitley, 1933. Holotype Australian Museum, Sydney, IA 2457, New South Wales, a misshapen skin, 960 mm. FL, preserved in formalin with most of the fins broken. Pectoral fin about 45 percent of fork length. Figured by Whitley (1933, pl. xi, fig. 1).

Characters

Pectoral fin very long, usually reaching nearly or quite to second dorsal finlet, usually 31 percent of fork length or longer (similar to *T. obesus*). Body depth greatest near dorsal and anal origins. A narrow white posterior margin on caudal fin. Anal finlets silvery or dusky.

Gill rakers 25–31 (similar to *T. obesus* and *T. albacares*).

Liver with striations on ventral surface, its three lobes subequal in length, vascular cones present on its dorsal side (as in *T. thynnus*, *T. maccoyii*, and *T. obesus*). Spleen located on left side, stomach on right. Straight intestine short, the first loop located at about half to two-thirds the distance between middle liver lobe and anus. Gall bladder exposed in ventral view along right side of straight intestine. Connective tissue on dorsal wall of body cavity much thickened posteriorly. Kidney short, without posterior "tail," reaching level of vertebrae 7–9.

Cutaneous arteries usually originating at level of vertebra 3–4, passing laterally between ribs 3 and 4, and branching between intermuscular bones 4 and 5 (as in *T. thynnus* and *T. maccoyii*); no posterior commissure. A single row of arterioles and venules arising from each main lateral cutaneous branch (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*) but from vertebral side of vessels. Post-cardinal vein absent (as in *T. thynnus* and *T. maccoyii*).

Posterior parasphenoid margin forming an acute angle (not as extreme as in large *T. thynnus* but more acute than in large *T. obesus*). Supraoccipital crest relatively slender and long, reaching at least to centrum of vertebra 3.

Anterior articulating (sphenotic) head of hyomandibula relatively long and narrow, proportion of length to least width 1.7–2.7. Metapterygoid relatively narrow, proportion of length of anteroventral margin to posteroventral margin 1.1–1.8. Quadrate relatively narrow, proportion of length to width of horizontal dorsal edge 2.1–2.7.

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. thynnus* and *T. tonggol*), appearing twisted and not extending strongly ventrad. First closed haemal arch on vertebra 10 (as in *T. thynnus*, *T. maccoyii*, and occasionally in other species), forming an angle of 45 degrees or less with the vertebral axis. All haemal prezygapophyses arising from centra, not from haemal arches. All haemal postzygapophyses less than one-fourth centrum length. Anteriormost ventrolateral foramina small, their width not greater than basal width of haemal spine. Least height of centrum of 36th vertebra 1.1–1.7, usually 1.4–1.6, in centrum length (similar to *T. albacares*), centrum commonly tapering, with least depth at anterior end (in the other species the vertebra is of nearly equal height throughout). Haemal spine of first caudal vertebra flattened, wing-like.

Nominal Species

Although no one seems to have reported any important differences between Atlantic and Pacific populations of *T. alalunga*, at least since Jordan and Evermann (1926), many recent authors still refer to the Pacific populations as *T. germo*. Even Jordan and Evermann (1926) admitted that the slight differences they noted in body proportions and coloration would probably not be valid when more specimens were examined. Our data on *T. alalunga* confirm the view that the Atlantic and Pacific populations belong to the same species. Godsil (1948) and Kurogane and Hiyama (1958a, 1959) found slight population differences within the Pacific, but intermingling of a significant portion of the eastern and western Pacific populations of *T. alalunga* was indicated by tag returns reported by Ganssle and Clemens (1953) and Blunt (1954), and demonstrated by more recent works, including those of Otsu (1960), McGray, Graham, and Otsu (1961), Clemens (1961, 1963) and Otsu and Uchida (1963).

Range

In the western Atlantic, *T. alalunga* is known from south of New England to southern Brazil. Squire (1963) presented seven records north of 40° N., the most northerly 42°18′ N., 64°02′ W. Le Danois

(1951) reported the species off the coast of Venezuela. Rodrigues Lima and Wise (1963) reported catches from 10° N. to 32° S. off the coast of Brazil, with a concentration near 15° S. There are no records for the Gulf of Mexico. In the eastern Atlantic, it has been found from the Orkney Islands north of Scotland (Clarke, 1900; Tucker, 1955), south to Angola off west African coast (Vilela and Monteiro, 1959) and in the Mediterranean Sea. The range may extend south to South Africa, because Talbot and Penrith (1962, 1963) have found a continuous distribution around South Africa. On the other hand, the South African population may be of Indian Ocean origin.

The distribution in the Indian and Pacific oceans was mapped by Yoshida and Otsu (1963) and by Suda, Koto, and Kume (1963). *T. alalunga* is found across the Indian Ocean from East Africa to Australia between about 10° N. and 30° S. Its range in the western Pacific extends from about 45° N., off the coast of Hokkaido, south to 40° S., off the southern tip of Australia. Longline fishing has indicated a fairly continuous distribution between 30° N. and 20° S., eastward past the Hawaiian Islands. In the eastern Pacific, it is known from about 50° N., off Vancouver Island, British Columbia (Cowan, 1938; Samson, 1940), south to about 42° S. (Japan Fishery Agency, 1964, 1965).

THUNNUS ALBACARES (Bonnaterre, 1788) YELLOWFIN TUNA

Albacores or *Thynni* Sloane, 1707: 11 (description; Madeira), fig. 1.

Scomber albacares Bonnaterre, 1788: 140 (original description based on drawing by Sloane).

Scomber albacorus Lacépède, 1800: 599 and 1802: 48–49 (substitute name for *Scomber albacares* Bonnaterre, 1788).

Thynnus argentivittatus Cuvier *in* Cuvier and Valenciennes, 1831: 97–98 (original description; Atlantic and Pacific). Günther, 1860: 366.

Scomber Sloanei Cuvier *in* Cuvier and Valenciennes, 1831: 148 (original description based on Sloane).

Thynnus albacora Lowe, 1839: 77–78 (original description; Madeira) and 1849: 2 (repeat of original description). Günther, 1860: 365. Cunningham, 1910: 110–112 (synonymy, description; St. Helena), fig. 4.

Thynnus macropterus Temminck and Schlegel, 1844: 98–99 (original description; Japan), pl. 51. Kishinouye, 1915: 19 (description, anatomy; Japan), pl. 1, fig. 12.

Thunnus argentivittatus, South, 1845: 622. Rivas, 1951: 221–222 (synonymy).

Orcynus subulatus Poey, 1875: 145–146 (original description; Cuba), pl. 3, fig. 4 (head), fig. 5 (scale).

Orcynus albacora, Poey, 1875: 145.

Orcynus macropterus, Kitahara, 1897: 2 (description; Japan), pl. 2, fig. 3.

Germo macropterus, Jordan and Snyder, 1901: 64 (Nagasaki). Jordan and Seale, 1906: 228 (Samoa). Jordan and Jordan, 1922: 32–33 (Hawaii).

Thunnus macropterus, Jordan et al., 1913: 121 (Japan). Kishinouye, 1915 (description, anatomy; Japan). de Beaufort, 1951: 223–225 (synonymy, description), fig. 39. Ginsburg, 1953: 8–10 (restriction of name *macropterus* to W. Pacific yellowfin).

Thunnus allisoni Mowbray, 1920: 9–10 (original description; Miami, Fla.), figure (unnumbered).

Germo argentivittatus, Nichols and Murphy, 1922: 507 (Peru).

Germo allisoni, Nichols, 1923: 3 (Christmas Island).

Neothunnus macropterus, Kishinouye, 1923: 446–448 (anatomy; Japan; placed in new genus *Neothunnus*), figs. 13, 19, 23, 45, 51. Jordan and Hubbs, 1925: 219 (Japan). Jordan and Evermann, 1926: 20–21 (description), pl. 5. Herre, 1936: 106–107 (synonymy; Galapagos, Philippines, Japan; no species differences between long- and short-finned yellowfin). Walford, 1937: 3–7 (description; Pacific Allison tuna merely old yellowfin), color pl. 33. Serventy, 1941: 25–26 (description; Australia), pl. 2. Godsil and Byers, 1944: 46–69 (anatomy; comparison of Pacific specimens), figs. 20–35, 70–76. Tinker, 1944: 159–160 (Hawaii), pl. 1, fig. 5. Godsil, 1948 (morphometry; Japan, Hawaii, E. Pacific). Schaefer, 1948 (morphometry; Pacific Costa Rica). Brock, 1949: 276 (key to Hawaiian tunas). Schaefer and Walford, 1950 (comparison of yellowfin from Angola and Pacific coast of Central America). Godsil and Greenhood, 1951 (comparison of E. and central Pacific specimens). Schaefer, 1952 (comparison of Hawaiian and W. Pacific specimens). Royce, 1953 (morphometry; Pacific; an east-west cline across the Pacific in some characters). Tsuruta, 1954 (morphometry; SW. Pacific). Schaefer, 1955 (comparisons of specimens from SE. Polynesia,

Central America, and Hawaii). Tsuruta, 1955 (morphometry; southwest Great Sunda Island; yellowfins probably a single worldwide species with many sub-populations). Kurogane and Hiyama, 1957a (morphometry; equatorial Pacific). Kurogane and Hiyama, 1958b (morphometry; Indian Ocean). Munro, 1958: 111 (Australia). Nakagome, 1958 (morphometry; Indian Ocean). Broadhead, 1959 (morphometry; E. tropical Pacific). Klawe, 1959 (reidentification of juvenile called *T. thynnus* by Fowler, 1944). Gosline and Brock, 1960: 260–261 (description; Hawaii), 337 (synonymy), fig. 257j. Jones and Silas, 1960: 385–386 (Laccadive Sea, Gulf of Mannar, Ratnagiri), fig. 12. Legand, 1960 (measurements, counts; New Caledonia; east-west cline in gill rakers across Pacific). Tsuruta and Tsunoda, 1960 (morphometry; Indian Ocean). Talbot and Penrith, 1962: 558 (S. Africa). Mimura et al., 1963a (biology; Indian Ocean). Talbot and Penrith, 1963: 617–623 (description, biology; S. Africa).

Thunnus subulatus, Jordan and Evermann, 1926: 11–12 (repeat of Poey's original description). Jordan et al., 1930: 260. Ginsburg, 1953: 6–8 (synonymy, description; the name *subulatus* used for W. Atlantic yellowfin). Fernandez-Yepez and Santaella, 1956: 6 (Venezuela; in key as a species of bluefin).

Neothunnus catalinae Jordan and Evermann, 1926: 19 (original description; Santa Barbara Islands, S. California), pl. 4. Jordan et al., 1930: 260. Nichols and La Monte, 1941: 31, fig. 1.

Neothunnus albacora, Jordan and Evermann, 1926: 21–22. Frade, 1929: 235–241 (morphometry, swimbladder; Canary Islands), pl. 5, fig. 2. Buen, 1930: 49–50, fig. 8. Bini, 1931: 31–36 (morphometry; Canary Islands), figs. 12, 13. Frade, 1931a: 123–126 (synonymy, morphometry; E. Atlantic). Nichols and La Monte, 1941: 30 (synonymy in part), fig. 2. Barnard, 1948: 378–380 (S. Africa), pl. 11. Bellón and Bardán de Bellón, 1949 (morphometry; Canary Islands). Morice, 1953: 71–73, fig. 5 (liver; E. Atlantic). Postel, 1955 (biology, morphometry; E. Atlantic). Fernandez-Yepez and Santaella, 1956: 15 (in key to Atlantic tunas). Marchal, 1959 (morphometry; E. Atlantic). Vilela and Monteiro, 1959: 30–53 (morphometry; Angola). Tsuruta, 1961 (morphometry; SW. Indian Ocean). Vilela and Frade, 1963 (biology; E. Atlantic).

Neothunnus itosibi Jordan and Evermann, 1926: 22–23 (original description; Hawaii), pl. 6. Smith, 1935: 207–209 (S. Africa), fig. 4. Phillips, 1932: 231 (New Zealand). Powell, 1937: 80–81 (New Zealand), pl. 17, figs. 2, 3. Jones and Silas, 1960: 387–388 (Madras; recognized as distinct from *N. macropterus*), fig. 13.

Neothunnus albacores, Jordan and Evermann, 1926: 23–24 (description). Jordan et al. 1930: 260. Fernandez-Yepez and Santaella, 1956: 17–18 (Venezuela), fig. 6, pl. 8.

Neothunnus allisoni, Jordan and Evermann, 1926: 24 (description). Jordan et al., 1930: 260. Nichols and La Monte, 1941: 30–31 (synonymy), fig. 3. Fernandez-Yepez and Santaella, 1956: 16 (Venezuela), fig. 5, pl. 7.

Kishinoella zacalles Jordan and Evermann, 1926: 27 (original description, Honolulu fish market), pl. 7.

Semathunnus guildi Fowler, 1933: 163–164 (original description; Tahiti), pl. 12.

Semathunnus itosibi, Fowler, 1933: 164. Tinker, 1944: 160 (Hawaii).

Neothunnus argentivittatus, Beebe and Tee-Van, 1936: 184–192 (synonymy, description; West Indies), fig. 5 (copy of fig. in Cunningham), figs. 6–12 (photographs), fig. 13 (copy of fig. in Sloane). Fowler, 1944: 498 (Mexico, Ecuador, Peru).

Germo albacora, Fowler, 1936: 623-624 (synonymy, description), fig. 282. Smith, 1949, 1953: 299 (S. Africa), pl. 66, fig. 835.

Thunnus albacora, Tortonese, 1939: 326 (off Brazil). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 144–145 (synonymy), fig. 7. Morrow, 1954: 16 (29 E. African specimens similar to Pacific specimens).

Germo itosibi, Smith, 1949, 1953: 299 (S. Africa), pl. 65, fig. 834.

Neothunnus albacora brevipinna Bellón and Bardán de Bellón, 1949: 12–19 (original description; as *Neothunnus albacora* forma *brevipinna;* Canary Islands).

Neothunnus albacora longipinna Bellón and Bardán de Bellón, 1949: 12–19 (new name for long-finned *T. albacares* of East Atlantic; as *Neothunnus albacora* forma *longipinna;* Canary Islands).

Neothunnus macropterus macropterus, Bellón and Bardán de Bellón, 1949: 15 (Pacific short-finned form; as *Neothunnus macropterus* forma *macropterus*).

Neothunnus macropterus itosibi, Bellón and Bardán de Bellón, 1949: 15 (Pacific long-finned form; as *Neothunnus macropterus* forma *itosibi*).

Neothunnus brevipinna, Postel, 1950: 67–74 (description, biology; considered a good species distinct from *N. albacora*).

Thunnus zacalles, Fraser-Brunner, 1950: 142 (key to *Thunnus*), 146, fig. 9.

Thunnus albacares, Ginsburg, 1953: 3–6 (synonymy, description; the name *albacares* restricted to the E. Atlantic yellowfin). de Sylva, 1955: 33–40 (osteology, relationships), fig. 58 (neurocranium). Bullis and Mather, 1956 (counts, measurements, key to Caribbean *Thunnus*), fig. 2. Mather and Gibbs, 1957:242 (off New England). Rivas, 1961: 136–139 (synonymy, range). Schaefer, Broadhead, and Orange, 1963 (biology; Pacific). Squire, 1963 (distribution; NW. Atlantic). Iwai and Nakamura, 1964: 6, figs. 3G, H (olfactory rosettes). Tsuruta, 1964: 59–66 (morphometry; Pacific and Indian oceans). Williams, 1964: 115–120 (E. Africa). Iwai et al., 1965: 11–15 (synonymy), 36–38 (description), figs. 20, 21. Nakamura, 1965: 20–22, figs. 3E, 9B, 10 (osteology). Royce, 1965 (morphometry). Merritt and Thorp, 1966: 375–376 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus catalinae, Ginsburg, 1953: 8 (name used for E. Pacific yellowfin).

Neothunnus albacares, Mather, 1954: 292 (SE. of New York). Mather and Day, 1954: 184–185 (N. Brazil and W. Africa).

Thunnus albacores, Le Danois, 1954: 283–287 (history of nomenclature), 285–286 (partial synonymy), 288-294 (biology; Pacific yellowfin recognized as *Thunnus albacores* variety *argentivittatus*).

Neothunnus albacora macropterus, Schultz, 1960: 414–415 (description of Bikini and Marianas specimens), pl. 122 A.

Thunnus albacares macropterus, Jones and Silas, 1963: 1793–1794 and 1964: 40–42 (Indian Ocean).

Thunnus itosibi, Jones and Silas, 1963: 1794–1795 and 1964: 42–43 (Indian Ocean).

Types of Nominal Species

Scomber albacares Bonnaterre, 1788. No type specimens. Original description based on Sloane (1707, pp. 11–12; table 1, fig. 1).

Scomber albacorus Lacépède, 1800. Substitute name for *Scomber albacares* Bonnaterre, 1788.

Thynnus argentivittatus Cuvier *in* Cuvier and Valenciennes, 1831. Syntypes MNHN A.5567 (a stuffed whole skin; collected in the Atlantic Ocean by Quoy and Gaimard) and A.5572 (a half skin, with glass eye, mounted on a board; sent by Dussumier from the Indian Ocean). A third specimen, A.5814, designated by Schaefer and Walford (1950) as lectotype, is not a syntype because it was not mentioned by Cuvier in the original description (cf. Bauchot and Blanc, 1961, p. 376; Blanc and Bauchot, 1964, p. 454). We have examined both syntypes and cannot be certain what species they represent (see discussion under Nominal Species).

Scomber sloanei Cuvier *in* Cuvier and Valenciennes, 1831. No type specimens. Original description clearly based on Sloane (1707), plate 1, fig. 1, but also referring to page 28, where Sloane refers to a different fish (*Scombrus major torosus*). Cuvier stated that *Scomber albacorus* Lacépède, 1800, is not the same as *Scomber sloanei*, because Lacépède's description refers to page 11 of Sloane. This, however, is the description of the fish, from the illustration of which Cuvier drew his description.

Thynnus albacora Lowe, 1839. No type specimens.

Thynnus macropterus Temminck and Schlegel, 1844. Original description clearly based on the specimen figured in plate 51, and not on the specimen in the Rijksmuseum van Natuurlijke Historie, Leiden, number 2552, considered by Boeseman (1947, 1964) as the holotype. In particular, Temminck and Schlegel refer to the long second dorsal and anal fins, which the presumed holotype (fork length 670 mm. as measured by Gibbs in 1962) is too small to have developed.

We believe that this specimen should not have been considered as holotype of this species. The specimen (a stuffed skin) is not a yellowfin tuna at all, but is *T. tonggol*. The pectoral fin is 22 percent of fork length and the snout to second dorsal distance is 50.7 percent, both characteristic of *T. tonggol*.

Since we do not believe this specimen was used in the original description and, therefore, is not a type, we are saved the necessity of having to consider the name *tonggol* Bleeker, 1851 as a junior synonym of *macropterus*, which has been used more often than has any other name for Pacific yellowfin tuna.

Orcynus subulatus Poey, 1875. No type specimens known to us. Original description from an 1,800-mm. specimen, of which the head is figured and might have been saved.

Thunnus allisoni Mowbray, 1920. No type specimen known to us. Original description from three specimens: one taken by spearing in Biscayne Bay, Miami, Fla. for which counts, proportions of body parts, and color are given, but the length noted as a

little larger than the second specimen; a second specimen, 5 feet 9 inches long (1,753 mm.), "taken in the Gulf Stream," but "badly torn by sharks"; and a third specimen weighing 135 pounds (61 kg.).

Neothunnus catalinae Jordan and Evermann, 1926. Type originally designated as "No. 597, Mus. Calif. Acad. Sci., a photograph of a fish taken off Santa Catalina Island, California," weight 157½ pounds (71 kg.). This photograph was published earlier as *Germo macropterus* by Jordan and Starks (1907: 69). The fish appears to be a mounted specimen.

Neothunnus itosibi Jordan and Evermann, 1926. Type originally designated as "No. 598, Mus. Calif. Acad. Sci., a photograph . . . of a specimen weighing 321 pounds in Honolulu market." The specimen is no longer extant.

Kishinoella zacalles Jordan and Evermann, 1926. Type originally designated as "No. 599, Mus. Calif. Acad. Sci., a photograph of a specimen examined in the Honolulu market . . ., 2¼ feet long, . . . weighing 14 pounds." The characters given in the key to species (p. 26) are based on the specimen photographed; the text description is based on another specimen. Jordan and Evermann described *zacalles* as lacking a swimbladder, and they and subsequent workers (Serventy, 1942; Fraser-Brunner, 1950) have placed it close to *T. tonggol*. Jordan and Evermann, however, gave for their *zacalles* a gill-raker count of 30, which is completely outside the known range for *T. tonggol* (19–28, Table 2). It is our experience that the swimbladder may be quite difficult to find in some specimens of most species of *Thunnus*, and we believe that Jordan and Evermann probably overlooked it in their specimens of *zacalles*. They can not have been describing *T. thynnus*, as this species has more gill rakers and a much shorter pectoral fin than they show in their photograph of *zacalles*. Of the three remaining Pacific species, *T. alalunga* may be quickly eliminated because it has a much longer pectoral fin and an entirely different coloration. *T. obesus* has a much larger eye than that shown for *zacalles*, and the swimbladder is well developed in all specimens that we observed. The description of *Kishinoella zacalles* fits *T. albacares* in number of gill rakers (mean for Pacific *T. albacares* 30.2, table 2), length of pectoral fin, coloration, and general body proportions. Also, Jordan and Evermann, in their original description, reported about a dozen specimens of *zacalles*, all from Hawaii, and no specimen of it (or of *T. tonggol*) has since been reported from there. In view of the great fishery and research program on tunas in the Pacific, it seems highly unlikely that a valid species has been overlooked.

Neothunnus albacora brevipinna Bellón and Bardán de Bellón, 1949. No type specimens. Original description based on 11 specimens from the Canary Islands.

Neothunnus albacora longipinna Bellón and Bardán de Bellón, 1949. No type specimens. Presumed to be a new subspecific designation for the typical subspecies of *N. albacora* Lowe (1839).

Semathunnus guildi Fowler, 1933. Holotype ANSP 55982, a dried skin with skull intact, from Tahiti. Fowler stated, "Length 1,830 mm." Our measurement of fork length was about 1,460 mm., of length to end of caudal lobes about 1,680 mm. The specimen is obviously a yellowfin tuna, with high dorsal and anal fins, and the pectoral reaching to the middle of the second dorsal base.

Characters

Pectoral fin intermediate in length, usually reaching beyond second dorsal origin but not beyond end of its base, usually 22–31 percent of fork length (generally similar to *T. atlanticus* and large *T. obesus*). Dorsal and anal fins very long in large specimens, becoming well over 20 percent of fork length.

Gill rakers 26–35 (overlapping with *T. alalunga* and *T. obesus*).

Liver without striations on ventral surface, its right lobe longer and narrower than the others; vascular cones not present on dorsal side (as in *T. atlanticus* and *T. tonggol*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*). Connective tissue on dorsal wall of body cavity thickened at anterior end to form a prominent raised cord. Kidney long, tapering, reaching level of vertebra 12–14, often with accessory masses posterior to main kidney.

Cutaneous artery usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, and branching between intermuscular bones 6 and 7 (as in *T. atlanticus* and *T. tonggol*) or 7–8. A single row of arterioles and venules arising from each main lateral cutaneous branch (as in *T. alalunga*, *T. tonggol*, and *T. atlanticus*) but from lateral sides of vessels (as in *T. tonggol* and *T. atlanticus*). Vessels present on each side parallel to dorsal aorta connecting posterior epibranchial to cutaneous artery. Postcardinal vein present, joining right cutaneous vein (as in *T. atlanticus*, *T. tonggol*, and *T. obesus*).

Posterior parasphenoid margin variable in shape, rounded, concave, or somewhat angulate (as in *T. atlanticus* and *T. tonggol*) but never with a pronounced angle.

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all *Thunnus* except *T. thynnus* and *T. tonggol*). First closed haemal arch usually on vertebra 11 (as in *T. atlanticus*, *T. tonggol*, *T. obesus* and often in *T. thynnus*). Anteriormost haemal prezygapophyses arising far ventrad on haemal arch (as in *T. atlanticus* and *T. tonggol*). Haemal postzygapophyses long (as in *T. atlanticus* and *T. tonggol*), the longest about 75 percent of its centrum length (somewhat shorter than in *T. atlanticus* and *T. tonggol*). Anteriormost ventrolateral foramina large, their width three or more times that of haemal spine (as in *T. atlanticus* and *T. tonggol*). Least height of centrum of 36th vertebra 1.2–1.9, usually 1.3–1.5 in centrum length (resembling *T. alalunga*, but in that species the vertebrae taper, whereas in *T. albacares* they are of nearly equal width throughout).

Nominal Species

More names have been proposed for supposedly different populations and individual variants of *T. albacares* than for all other species in the genus. Jordan and Evermann (1926) took the most extreme position in recognizing seven species: *catalinae*, from the California coast; *macropterus*, from the central and western Pacific; *itosibi*, a long-finned form from Hawaii and Japan; *albacora*, from the eastern Atlantic; *albacores*, from Madeira and the West Indies; *allisoni*, a western Atlantic long-finned form; and *zacalles* from Hawaii (which has heretofore been considered as most closely related to *T. tonggol*, see above). The main characters that they used to separate these forms were the lengths of the second dorsal and anal lobes. Using the same characters, Ginsburg (1953) distinguished an eastern Atlantic *albacares*, a western Atlantic *subulatus*, an eastern Pacific *catalinae*, and a central and western Pacific *macropterus*. It became apparent to us that *T. albacares* is an extremely variable species morphometrically, from our own data and from the many detailed morphometric studies on populations of *T. albacares*, especially in the Pacific, by workers such as Godsil (1948), Schaefer (1948, 1952, 1955), Schaefer and Walford (1950), Godsil and Greenhood (1951), Royce (1953), Tsuruta (1954, 1955, 1961), Kurogane and Hiyama (1957a, 1958b), Nakagome (1958), Broadhead (1959), Legand (1960), and Frade (1931a, for the eastern Atlantic).

Statistical analysis of morphometric data indicates that many subpopulations of *T. albacares* are differentiated, but certainly not to a species or subspecies level. Royce (1965), in a monumental study of the morphometry of *T. albacares*, showed conclusively that it is a single, locally variable, pantropical species. He found that the differences between eastern Atlantic and eastern Pacific specimens were less than the differences between eastern Pacific and Caroline Islands specimens, and that several characters change clinally from west to east in the equatorial Pacific.

There has been considerable confusion concerning the name *Thynnus argentivittatus* Cuvier. The original description (Cuvier, *in* Cuvier and Valenciennes, 1831: 97–98) was based on two specimens now at the MNHN in Paris: one from the Atlantic, collected by Quoy and Gaimard (MNHN A.5572) and one from the Indian Ocean, sent by Dussumier (MNHN A.5567). Schaefer and Walford (1950) reported that, according to information received from L. Bertin, the description was based on three specimens: the two already mentioned and a third from the Indian Ocean, coast of Malabar, sent by Dussumier (MNHN A.5814; given erroneously as A.5816 by Schaefer and Walford). A.5814, a specimen in alcohol, was designated the lectotype by Schaefer and Walford (1950, p. 441), who thus recognized the Indian Ocean yellowfin as *Neothunnus argentivittatus*, the Pacific form as *N. macropterus*, and the Atlantic form as *N. albacora*. Based on A.5814 being the lectotype, Rivas (1961) used the name *argentivittatus* for an Indian Ocean tuna which he tentatively placed in the subgenus *Parathunnus*, and regarded as different from *Neothunnus albacares*, the yellowfin tuna, which he considered to be a single, pantropical species.

We have examined the supposed lectotype (A.5814) and believe it, and the other specimens in Rivas' (1961) account, actually to be *T. tonggol*. Watson (1964) reached the same conclusion, and suggested that *T. argentivittatus* be synonymized with *T. tonggol*. This action, to begin with, is inappropriate, for *argentivittatus* has priority over *tonggol*. A.5814, however, cannot be considered as the lectotype of *Thynnus argentivittatus*, as it is nowhere men-

tioned by Cuvier in the original description, whereas the two proper syntypes are noted (Bauchot and Blanc, 1961, p. 376; Blanc and Bauchot, 1964, p. 454). The lectotype must be selected from A.5567, a stuffed whole specimen, and A.5572, a dried half specimen mounted on a board. Although both of us examined the two syntypes and independently made counts and measurements, we do not feel that we can make a selection. Even if the appropriate measurements could be considered accurate, which they certainly cannot, they do not indicate that the syntypes are *T. albacares*, but rather leave the possibility that they could be *T. tonggol* or *T. atlanticus*. The distance from snout to second dorsal origin appears to eliminate *T. thynnus*, *T. alalunga*, and *T. obesus* from consideration. We do not believe that these specimens can be definitely identified, unless a new and better character is found.

Range

As Royce (1965) has shown, *T. albacares* is a pantropical species. In the western Atlantic, it is known from about 42° N. (Squire, 1963) south through the Sargasso Sea to the Gulf of Mexico and the Caribbean Sea (Wathne, 1959) and off the coast of South America from about 10° N. to 32° S. (Rodrigues Lima and Wise, 1963). In the eastern Atlantic, it is recorded from the coasts of Spain and Portugal south to Angola (Vilela and Monteiro, 1959; Vilela and Frade, 1963) but not from the Mediterranean Sea. Talbot and Penrith (1962, 1963) have shown that *T. albacares* has a continuous distribution around South Africa, but the origin of these fish is uncertain.

It is abundant in East African waters (Williams, 1964) and is known from 20° N. to 30° S. in the Indian Ocean (Mimura et al., 1963a). In the western Pacific *T. albacares* occurs from 40° N., off the coast of Japan, to 30° S., off the coast of Australia, between the 70° F. September isotherm to the north and 75° F. February isotherm to the south (Schaefer et al., 1963). The distribution extends across the Pacific in a broad belt from about 30° N. to 20° S., between the same isotherms, and as far as 40° S. (Japan Fishery Agency, 1965).

THUNNUS ATLANTICUS (Lesson, 1830) BLACKFIN TUNA

Thynnus atlanticus Lesson, 1830: 165–166 (original description; Trinidade Is. off Brazil). Günther, 1860: 362 (in footnote as dubious species).

Thynnus coretta Cuvier *in* Cuvier and Valenciennes, 1831: 102–104 (original description; Martinique). Günther, 1860: 363.

Thynnus balteatus Cuvier *in* Cuvier and Valenciennes, 1831: 136–137 (original description based on Lesson's unpublished drawing).

Thunnus balteatus, South, 1845: 622.

Thunnus coretta, South, 1845: 622 (description). Jordan and Evermann, 1926: 11 (description). Jordan et al., 1930: 260.

Orcynus balteatus, Poey, 1868: 361–362 (Cuba). Poey, 1875: 145 (Cuba).

Parathunnus rosengarteni Fowler, 1934: 354, 356 (original description; Key Largo, Fla.), figs. 3–5.

Parathunnus ambiguus Mowbray, 1935 (original description; Bermuda).

Parathunnus atlanticus, Beebe and Hollister, 1935: 213–214 (Union Is., British West Indies). Beebe and Tee-Van, 1936: 178–184 (synonymy, description; Bermuda and West Indies), figs. 1–4. Fowler, 1944: 102–103 (synonymy, description; W. Caribbean), fig. 149. Schuck and Mather, 1951: 248 (N. Carolina). Mather and Schuck, 1952: 267 (Martha's Vineyard; NW. Caribbean). Mather and Day, 1954: 183–184 (off coasts of Brazil and Bermuda).

Thunnus atlanticus, Rivas, 1951: 219–220 (synonymy, description). de Sylva, 1955 (osteology, relationships, generic status), figs. 1–54, 57 (osteology). Bullis and Mather, 1956 (counts, measurements, key to Caribbean *Thunnus*). Rivas, 1961: 129–131 (synonymy, description). Iwai et al., 1965: 15–16 (synonymy), 38–39 (description), fig. 22. Nakamura, 1965: 23–24, figs. 3F, 9C, 11 (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Misidentifications

The specimen reported as *Parathunnus obesus* by Beebe and Tee-Van (1928: 100) from Haiti is *T. atlanticus* as they (Beebe and Tee-Van, 1936: 181) later pointed out. Fernandez-Yepez and Santaella (1956: 19) reported specimens from Venezuela as *Parathunnus obesus*, but these are probably *T. atlanticus* as indicated by Rivas (1961: 130).

The International Game Fish Association (1965) listed the world record *T. atlanticus* as a 44 pound, 8 ounce, specimen from Cape Town, South Africa. This record is obviously in error and has been corrected (1966).

Types of Nominal Species

Thynnus atlanticus Lesson, 1830. No type specimens. Original description based on a specimen 28 inches total length (711 mm.), with a pectoral fin 6 inches long (152 mm.). Subtracting 50 mm., we obtain a fork length of about 660 mm. The pectoral is about 23 percent of fork length; too short for either *T. albacares* or *T. atlanticus* (see fig. 26), but is nearer the latter. Lesson mentioned only two other characters useful in identifying the species: a coppery-red lateral band, and blue-slate colored fins (presumably also finlets). These appear sufficient to associate the name *atlanticus* with the blackfin tuna, and we follow Beebe and Tee-Van (1936) and later authors in doing so.

Scomber coretta Cuvier, 1829. No type specimen. The first use of the name *coretta* for a tuna is usually credited to Cuvier *in* Cuvier and Valenciennes (1831), where he described *Thynnus coretta*. The original description, however, consists of a footnote on page 198 of the second edition of Règne Animal (1829), which refers only to Sloane (1707, vol. 1, plate 1, fig. 3). Sloane's figure is of "*Scomber Major torosus*," and there is no way of associating it with any known species, but this indication prevents the name from being considered a nomen nudum. *Scomber coretta* Cuvier, 1829 must be regarded as a nomen dubium.

Thynnus coretta Cuvier *in* Cuvier and Valenciennes, 1831. This later use of the name *coretta* is based on a preserved specimen, MNHN A.5380, 263 mm. fork length from Martinique. It is a blackfin tuna with 19+20 vertebrae and a gill-raker count of 6+17 (left) and 7+17 (right).

Thynnus balteatus Cuvier *in* Cuvier and Valenciennes, 1831. No type specimens. Original description based on an unpublished illustration by Lesson of the same specimen from which *Thynnus atlanticus* was described, and, therefore, a synonym of that species.

Parathunnus rosengarteni Fowler, 1934. Holotype ANSP 60174, a stuffed skin 629 mm. fork length. A count of gill rakers was impossible, but our measurements show the pectoral fin to be 25.8 percent of fork length, characteristic of *T. atlanticus*.

Parathunnus ambiguus Mowbray, 1935. No type specimens. Original description based on Bermuda specimens; gill rakers noted as 6+17, swimbladder "simple, broader than long, well forward," finlets dusky with a trace of yellow. These characters unquestionably refer this nominal species to the synonymy of *T. atlanticus*.

Characters

Pectoral fin intermediate in length (generally similar to *T. albacares* and large *T. obesus*), usually 22–31 percent of fork length. Dorsal and anal finlets in fresh specimens lacking yellow.

Gill rakers 19–25, resembling only *T. tonggol*.

Liver without striations on ventral surface, right lobe long and narrow, no vascular cones on dorsal surface (as in *T. albacares* and *T. tonggol*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*).

Swimbladder either small, oblate, situated far anteriorly, or resembling a poorly developed *T. albacares;* when long, anterior and posterior chambers divided by a membrane.

Cutaneous arteries usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, branching between intermuscular bones 6 and 7 (as in *T. albacares, T. tonggol,* and *T. obesus*). A single row of arterioles and venules arises from each main lateral cutaneous branch (as in *T. albacares, T. tonggol,* and *T. alalunga*), but from the lateral side of each vessel (as in *T. albacares* and *T. tonggol*). Postcardinal vein present, joining right cutaneous vein (as in *T. albacares, T. tonggol,* and *T. obesus*).

Posterior parasphenoid margin rounded, concave, or somewhat angulate (as in *T. albacares* and *T. tonggol*), never with a pronounced angle. Parasphenoid concave in its anterior portion (seen occasionally in small specimens of all other species).

Vertebrae 19+20, with rare exceptions. First ventrally directed parapophysis on vertebra 9 (as in all except *T. tonggol* and *T. thynnus*). First closed haemal arch usually on vertebra 11 (as in all except *T. alalunga* and some *T. thynnus*). Haemal arches narrow, bowing widely, forming a large, ovate canal (as in *T. tonggol*). Anterior haemal prezygapophyses arising far ventrad on haemal arch (as in *T. tonggol* and *T. albacares*). Longest haemal postzygapophyses equal to or longer than centrum (only *T. tonggol* and *T. albacares* approach this). Anteriormost ventrolateral foramina large, more than three times width of haemal spine (as in *T. albacares* and *T. tonggol*).

Nominal species

Beebe and Tee-Van (1936) established the validity of *T. atlanticus* and placed *Thynnus balteatus, Para-*

thunnus rosengarteni, and *P. ambiguus* in its synonymy. *Thynnus coretta*, which was placed in the synonymy of *T. thynnus* by Fraser-Brunner (1950) and Rivas (1951), is also a synonym of *T. atlanticus*, as Rivas (1961) has recently shown. Morice (1953), Frade (1960), and others have mistakenly plac Ted. *atlanticus* in the synonymy of *T. obesus*.

Range

Thunnus atlanticus is known only from the western Atlantic, from off Martha's Vineyard, Mass. (Mather and Schuck, 1952), and Cape Hatteras (Schuck and Mather, 1951), throughout the West Indies (Beebe and Tee-Van, 1936) and the northern Caribbean (Bullis and Mather, 1956), south to Trinidade Island off the coast of Brazil (Lesson, 1830) and off Rio de Janeiro at 22°21′ S., 37°37′ W. (Mather and Day, 1954).

THUNNUS OBESUS (Lowe, 1839) BIGEYE TUNA

Thynnus obesus Lowe, 1839: 78 (original description; Madeira). Lowe, 1849: 2 (copy of original description). Günther, 1860: 362 (in footnote as dubious species). Cunningham, 1910: 112 (synonymy, description; St. Helena), fig. 5.

Thynnus sibi Temminck and Schlegel, 1844: 97–98 (original description; Japan), pl. 50. Günther, 1860: 362 (in footnote as dubious species).

Orcynus sibi, Kitahara, 1897: 1–2 (description; Japan), pl. 1, fig. 2.

Thunnus sibi, Jordan and Snyder, 1901: 64 (*Germo sibi;* Nagasaki), 125 (supplementary note: the "Shibi" should be a species of *Thunnus*, *T. sibi*). de Beaufort, 1951: 222–223 (synonymy, description). de Sylva, 1955: 34–40 (osteology, relationships), fig. 59 (neurocranium). Rivas, 1961: 135–136 (synonymy, description; a valid Indo-Pacific species).

Germo sibi, Jordan and Snyder, 1901: 64 (listed; in supplementary note, p. 125 as *Thunnus sibi*). Jordan and Jordan, 1922: 33 (Hawaii).

Thunnus mebachi Kishinouye, 1915: 19 (original description; Japan).

Parathunnus mebachi, Kishinouye, 1923: 442–445 (description, anatomy; placed in the new genus *Parathunnus*), figs. 4, 22, 47, 49. Godsil and Byers, 1944: 104–119 (anatomy; E. Pacific). Mimura et al., 1963b (biology; Indian Ocean).

Parathunnus sibi, Jordan and Hubbs, 1925: 218 (description; Japan). Jordan and Evermann, 1926: 17 (description), pl. 3, fig. 2. Tinker, 1944: 159 (Hawaii). Brock, 1949 (description; Hawaii). Shimada, 1954 (distribution in Pacific). Gosline and Brock, 1960; 261 (description; Hawaii), 337 (synonymy). Alverson and Peterson, 1963 (biology; Pacific).

Parathunnus obesus, Jordan and Evermann, 1926: 17 (description). Frade, 1929: 229–235 (morphometry, swimbladder; Canary Is.), pl. 5, fig. 1. Buen, 1930: 50, (Spain) fig. 9. Bini, 1931: 27–30 (morphometry; Canary Is.). Frade, 1931a (morphometry, swimbladder; E. Atlantic). Beebe and Tee-Van, 1936: 181 (comparison with *T. atlanticus*). Morice, 1953: 70–71, fig. 4 (liver; E. Atlantic.) Frade, 1960: 1–74 (description, distribution, biology, bibliography), pl. 1–7.

Thunnus obesus, Fraser-Brunner, 1950: 142 (key to *Thunnus*), 144 (synonymy, in part), fig. 6. Rivas, 1951: 220 (comparison with *T. atlanticus* and *T. alalunga*). Bullis and Mather, 1956 (counts, morphometry, key to Caribbean species of *Thunnus*), fig. 2. Mather and Gibbs, 1958: 23 (NW. Atlantic). Rivas, 1961: 133–135 (description, synonymy; restricted to Atlantic). Talbot and Penrith, 1961: 240 and 1962: 558 (S. Africa). Talbot and Penrith, 1963: 624–629 (description, biology; S. Africa). Iwai and Nakamura, 1964: 6, fig. 3B (olfactory rosettes). Iwai et al., 1965: 9–11 (synonymy), 34–36 (description), fig. 19. Nakamura, 1965: 18–19, figs. 3D, 8, 9A (osteology). Merritt and Thorp, 1966: 376–377 (E. Africa). Nakamura and Kikawa, 1966 (infracentral grooves).

Parathunnus obesus mebachi, Jones and Silas, 1960: 383–384 (Indian Ocean), fig. 10.

Thunnus obesus sibi, Jones and Silas, 1963: 1791–1792 (Indian Ocean).

Thunnus obesus mebachi, Jones and Silas, 1964: 36–38 (Indian Ocean).

Misidentification

The 1,450-mm. specimen reported as *T. thynnus* by Fernandez-Yepez and Santaella (1956) is probably *T. obesus* as indicated by Mather and Gibbs (1958: 238) and by Rivas (1961: 134).

Types of Nominal Species

Thynnus obesus Lowe, 1839. No type specimens. Original description rather vague, but definitely referring to the species as now recognized. Apparently based on large specimens from Madeira. Differentiated from *T. thynnus* (as *Thynnus vulgaris*)

"by the larger eye and shorter thickset figure." Pectoral fins described as reaching end of second dorsal fin, longer than in *T. albacares* (as *Thynnus albacora*).

Thynnus sibi Temminck and Schlegel, 1844. Lectotype, RMNH 2327 (a mounted skin, 600 mm. fork length), and paralectotype, RMNH 799 (right side of mounted skin, backed by cardboard, 557 mm. fork length) designated by Boeseman (1947). Measurements made by Gibbs in 1962 fall in the range of *T. albacares* rather than *T. obesus*, but mounted specimens could be expected to be unreliable for this purpose. The description by Temminck and Schlegel likewise offers little aid in identifying the species. They note that the pectoral fin is shorter than in *T. alalunga* (as *Thynnus alalonga* or *T. pacificus*) and approaches in length that of *T. albacares* (as *T. argentivittatus*), and their illustration shows a pectoral fin resembling that of a fairly small Pacific *T. obesus*. On this basis, we follow other authors in considering *T. sibi* a synonym of *T. obesus*. If the measurements of the lectotype and paralectotype were taken at face value, *T. sibi* would have to be regarded as a synonym of *T. albacares*, but we prefer for the present to disregard these specimens.

Thunnus mebachi Kishinouye, 1915. No type specimens. Original description clearly referable to *T. obesus*, apparently based on a number of specimens.

Characters

Pectoral fin intermediate in length (22–31 percent of fork length) in specimens longer than 1,100 mm. (as in *T. albacares* and *T. atlanticus*), as long as in *T. alalunga* (greater than 31 percent) in specimens less than 1,100 mm. from the Pacific.

Gill rakers 23–31 (generally similar to *T. albacares* and *T. alalunga*).

Liver with striations on ventral surface (not restricted to margins, fig. 30), its three lobes subequal in length, vascular cones present on its dorsal side (as in *T. thynnus*, *T. maccoyii*, and *T. alalunga*). Spleen on right side, stomach on left (as in all except *T. alalunga*). Swimbladder as long as body cavity, with two globular dorsal heads anteriorly, tapering gradually to a point posteriorly. Kidney with a short tail, reaching the level of vertebra 11–13.

Cutaneous artery usually originating at level of vertebra 6–8, passing laterally between ribs 5 and 6, branching between intermuscular bones 6 and 7 (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. thynnus* and *T. maccoyii*). Post-cardinal vein present, joining right cutaneous vein (as in *T. albacares*, *T. tonggol*, and *T. atlanticus*).

Posterior parasphenoid margin either rounded (in some small specimens) or forming a slightly obtuse angle (not as acute as in *T. alalunga*, *T. maccoyii*, or *T. thynnus*).

Vertebrae 18+21 (as in all *Thunnus* except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. tonggol* and *T. thynnus*). First closed haemal arch usually on vertebra 11 (as in *T. albacares*, *T. atlanticus*, *T. tonggol*, and some *T. thynnus*). Haemal prezygapophyses arising high on haemal arch (as in *T. thynnus* and *T. maccoyii*). All haemal postzygapophyses short, less than half centrum length (as in *T. alalunga*, *T. thynnus*, and *T. maccoyii*). Anteriormost ventrolateral foramina small, not more than 1½ times width of haemal spine (as in *T. alalunga*, *T. thynnus*, and *T. maccoyii*).

Nominal species

Three names have been applied to this species: *Thunnus obesus* for the Atlantic population and *T. sibi* and *T. mebachi* for the Pacific population, both latter names based on Japanese specimens. Fraser-Brunner (1950) correctly placed *sibi* and *mebachi* in the synonymy of *T. obesus* but also mistakenly included *Thunnus maccoyii*, *T. phillipsi* (= *T. maccoyii*), and *Parathunnus rosengarteni* (= *T. atlanticus*) as was pointed out by Rivas (1961). Jones and Silas (1960) stated that they could find no notable differences between Atlantic and Pacific populations, but referred to their Indian Ocean specimens as *Parathunnus obesus mebachi*. Because the name *sibi* has priority over *mebachi*, this should be *T. obesus sibi* if the Indo-Pacific population is subspecifically differentiated, and the latter name was used by Jones and Silas (1963).

Rivas (1961) claimed that the Pacific populations ("*sibi*") can be distinguished from the Atlantic *T. obesus* at lengths of about a meter by a much longer pectoral fin, but admitted difficulty in differentiating large specimens. His conclusion was based on a single small Atlantic specimen (746 mm., pectoral 29.4 percent of fork length) and 10 small specimens (data from Dung and Royce, 1953: 74) from the western Marshall Islands (600–835 mm., pectoral 38.8–44.9 percent).

FIGURE 30.—Livers of Atlantic *Thunnus obesus*, ventral view. (Top) from specimen 715 mm. fork length; (bottom) from specimen 1,433 mm. fork length (photographed by P. C. Wilson).

Although abundant data are available for Pacific *T. obesus* from 400 mm. and up (Dung and Royce, 1953), very few Atlantic specimens smaller than 1,000 mm. have been recorded. These data, nevertheless, indicate that the pectoral fin in Atlantic *T. obesus* does not become as long as that of the Pacific populations and that, in fact, the length of this fin in Atlantic *T. obesus* approaches *T. albacares* more closely than Pacific *T. obesus* at intermediate sizes (650–1,000 mm). Some Pacific and Indian Ocean specimens, however, have shorter pectorals than the majority and overlap with Atlantic specimens (fig. 31).

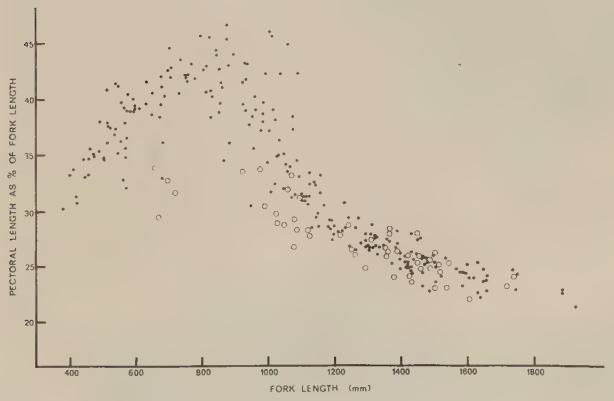


FIGURE 31.—Relative length of pectoral fin in *Thunnus obesus*. Dots, Indian and Pacific ocean specimens; open circles, Atlantic specimens.

It seems, therefore, that the Atlantic population of *T. obesus* is differentiated from the Pacific population, perhaps on a subspecific level, but much more data on sizes smaller than 1,000 mm. will be necessary to establish the level of differentiation.

Range

The distribution of *T. obesus* in the western Atlantic, as summarized by Mather and Gibbs (1958), includes the area from 42°18′ N., 64°02′ W. south along the coast of the United States to Florida; Bermuda; the Caribbean Sea around the West Indies; south to Margarita Island, Venezuela (reported as *T. thynnus* by Fernandez-Yepez and Santaella, 1956, but considered to be *T. obesus* by Mather and Gibbs). Nagai and Nakagome (1958) reported *T. obesus* from the north equatorial and Brazil currents off the coast of South America. In the eastern Atlantic it has been taken off Portugal, Spain, the Azores, and Madeira, south to Angola (Vilela and Monteiro, 1959) but it is absent from the Mediterranean Sea. There is a report of its occurrence from the Gulf of Gascogne (Legendre, 1936), but this needs confirmation. Talbot and Penrith (1961, 1962, 1963) have shown the distribution to be continuous around the tip of South Africa, but the fish could originate either in the Atlantic or Indian ocean.

T. obesus, like *T. albacares*, is found throughout the Indian Ocean from 20° N. to 30° S. (Mimura et al., 1963b). Its range in the western Pacific is also similar to that of *T. albacares*, extending from about 40° N. to about 30° S. (Alverson and Peterson, 1963). In the eastern Pacific it extends to 40° S. (Japan Fishery Agency, 1965).

THE BLUEFIN TUNA COMPLEX: *T. MACCOYII* AND *T. THYNNUS*

In recent years, various authors have attempted to recognize as distinct species the populations of bluefin tuna in Japan and the western Pacific (*T. orientalis*), Australia (*T. maccoyii*), eastern Pacific (*T. saliens*), western Atlantic (*T. secundodorsalis*), and eastern Atlantic (*T. thynnus*). Frade (1925) noted that the eastern Atlantic form had two rows of cutaneous arterioles, whereas Kishinouye (1923) pictured a single row in his Japanese specimen. Godsil and Byers (1944) found California bluefin similar to Kishinouye's descriptions of the form, except for two major characters. According to Kishinouye, the swimbladder of the Japanese form is short, broad, and heart-shaped, whereas that of California specimens "is rudimentary and of a different shape in small fish, and so erratic in large specimens that no constant pattern is discernible" (Godsil and Byers, 1944: 102). In California specimens, there are two rows of cutaneous arterioles and, according to Kishinouye, but a single row in Japanese fish. Godsil and Holmberg (1950) described numerous anatomical differences among California, Australian, and western Atlantic specimens, finally concluding that the Australian form (*T. maccoyii*) is distinct from the California and western Atlantic forms (*T. thynnus*) and that the latter are also distinct, but not quite so trenchantly. On the basis of published accounts of Japanese and eastern Atlantic populations (Kishinouye, 1923; Frade, 1925), Godsil and Holmberg tentatively concluded that eastern and western Atlantic forms are conspecific but that the Japanese form is different. On the basis of

counts and measurements, Ginsburg (1953) recognized as species the eastern Atlantic, western Atlantic, and eastern Pacific populations but did not consider those from other geographic regions. Serventy (1956a) recognized only a single worldwide species, pointing out the ontogenetic increase in relative size of the swimbladder and suggesting that other distinguishing characters shown by Godsil and Holmberg (1950) may also be eliminated when size differences are considered. Serventy (1956a) suggested, however, that the populations from European seas, North American Atlantic coast, South Africa, North American Pacific coast, Asiatic coast of the North Pacific, and Australia-New Zealand, respectively, each be recognized as subspecies, largely on the basis of modal differences in gill-raker counts. We have previously recognized a single species with only two subspecies (Collette and Gibbs, 1963). Iwai et al., (1965) considered *T. maccoyii* and *T. thynnus* as distinct species, with no commitment as to subspecies of the latter.

When individual and ontogenetic variations are considered, almost every anatomical, morphometric, and meristic character has proved to be similar in all populations. The only exceptions are the number of gill rakers, length of pectoral fin, a few skeletal characters, the shape of the dorsal wall of the body cavity, and the color of the caudal peduncle keels. On the basis of these characters, we tentatively recognize two species of bluefin tuna: *T. maccoyii*, mainly from the Southern Ocean south of about 30° S., but including an area off northwestern Australia; and *T. thynnus*, with one subspecies, *T. t. thynnus*, in the Atlantic, and another, *T. t. orientalis* in the Pacific.

We were long reluctant to recognize *T. maccoyii* as a separate species, and even now we do so only with reservation. The only convincing characters that provide evidence of species status are the position of the first ventrally directed parapophysis (on the 9th vertebra in *T. maccoyii*, as opposed to the 10th, in *T. thynnus*) and the color of the fleshy caudal keels (yellow in *T. maccoyii*, dark in *T. thynnus*). The few other characters, none of them affording complete separation, are given in table 5.

The presence of *T. thynnus orientalis* in the southeastern Pacific and the northeastern Indian Ocean (Nakamura and Warashina, 1965), and of *T. thynnus thynnus* off Cape Town (Talbot and Penrith, 1963) in the same geographical areas as *T. maccoyii* gives biological support to considering *T. maccoyii* as a separate species, although it is not known whether the two actually spawn in the same areas.

Differences in the configuration of the dorsal wall of the body cavity are not apparent in specimens less than about 1,300 mm. As described by Godsil and Holmberg (1950), numerous western Atlantic specimens (*T. t. thynnus*) examined by us in the field and laboratory had a wide anterior bulge without a lateral concavity and had a deep, narrow trough lateral to the bulge (fig. 32). Our only large specimen of *T. maccoyii* (1,450 mm.) was similar to the western Atlantic forms. Eastern Pacific specimens of *T. t. orientalis*, 1,390 and 1,450 mm., confirm the differences described by Godsil and Holmberg. The anterior bulge is comparatively narrow, with a lateral concavity, and with a wide trough lateral to the bulge (fig. 32). Although we have dissected no large Japanese specimens, we are confident they will resemble those from the eastern Pacific.

Godsil and Holmberg (1950) eliminated a large number of characters from systematic consideration. We can substantiate almost all of their conclusions, and our observations invalidate most of their remaining differential characters.

The tubules of the caecal mass of *T. t. thynnus* and *T. t. orientalis* were said to be relatively large and

TABLE 5.—*Comparison of* Thunnus maccoyii *and the subspecies of* T. thynnus

[Mean values given in parentheses]

Character	*T. t. thynnus*	*T. t. orientalis*	*T. maccoyii*
Number of gill rakers	34–43 (38. 9) 8	32–40 (35. 9) 8	31–40 (33. 7) 9
First ventrally directed parapophysis on vertebra number			
9th vertebra: parapophysis height/least distance apart	1. 2–29. 6 (8. 1)	1. 1–12. 7 (4. 1)	0. 8–3. 2 (1. 6)
10th vertebra: canal height/least width of processes	1. 9–5. 4 (3. 5)	1. 0–9. 0 (4. 1)	6. 0–15. 9 (11. 3)
10th vertebra: canal height/canal width	1. 5–3. 2 (2. 2)	1. 4–4. 8 (2. 0)	0. 9–1. 7 (1. 3)
Depth of anterior haemal canals	first increase, then decrease	first increase, then decrease	decrease
Shape of dorsal wall of body cavity in large specimens	wide bulge with no lateral concavity; deep, narrow lateral trough	narrow bulge with lateral concavity; wide lateral trough	wide bulge with no lateral concavity; deep, narrow lateral trough
Pectoral length as percent fork length (600–1, 000 mm.)	17. 0–21. 7	16. 8–20. 8	20. 2–23. 0
Color of caudal keels	dark	dark	yellow

FIGURE 32.—Dorsal wall of body cavity of *Thunnus thynnus*. Ventral view with viscera removed and head end to the left. Left: *T. t. orientalis*, 1,450 mm. fork length, from California, showing the comparatively narrow anterior bulge with lateral concavity and wide lateral trough. Right: *T. t. thynnus*, 1,850 mm. fork length, from the western North Atlantic, showing the wide anterior bulge without a lateral concavity.

coarse compared with *T. maccoyii*. We could detect no differences.

The caecal mass is so variable in size that its dimensions cannot be used to differentiate populations.

The relative length of the lateral liver lobes of western Atlantic specimens encompasses the differences in lobe lengths suggested by Godsil and Holmberg.

The stomach length cannot logically be used as a specific character, since this is a highly distensible organ, the dimensions of which will vary under different physiological states.

Swimbladder dimensions vary with size, becoming larger with growth, as shown by Serventy (1956a) for *T. maccoyii* from Australia and by us for western Atlantic *T. t. thynnus* and eastern Pacific *T. t. orientalis*. Abe (1955) reported that the swimbladder was well developed in a 1,470-mm. specimen thought to be *T. maccoyii* from the eastern Indian Ocean. Kishinouye (1923) and Frade (1925) illustrated swimbladders for western Pacific and eastern Atlantic specimens, respectively, that are very similar to those of larger specimens from other regions, and Kishinouye noted that the swimbladder is short and very narrow in immature specimens of Japanese *T. thynnus orientalis*, but short and wide in adults.

Godsil and Holmberg described the posterior end of the kidney of *T. maccoyii* specimens as truncate. This condition was observed in several specimens of western Atlantic *T. t. thynnus*, which displayed all variations that have been described, but our specimens of *T. maccoyii* did not show this condition.

The branching of the ureter of *T. maccoyii* was said to differ in that the branching occurred well anterior in the kidney mass. We observed this condition in both *T. t. thynnus* and *T. t. orientalis;* in

two of our three specimens of *T. maccoyii* the branching occurred near the end of the tail of the kidney.

In *T. maccoyii*, the dorsal aorta was reported to be usually conspicuously constricted behind the origin of the cutaneous arteries. We observed this condition in both *T. t. thynnus* and *T. t. orientalis*, but size did not decrease in our specimens of *T. maccoyii*.

The presence of a connecting branch between the two main branches of the coeliacomesenteric artery was said to distinguish *T. t. orientalis* and *T. maccoyii* from *T. t. thynnus;* however, Godsil and Holmberg (1950) did not find the branch in one Australian specimen and they were uncertain as to its presence in another. Furthermore, we observed this connection in several western Atlantic specimens.

The cutaneous artery in *T. maccoyii* was said to pass laterally most often between ribs 2 and 3 (rather than 3 and 4) and to divide usually between intermuscular bones 5 and 6 (rather than 4 and 5). Godsil and Byers (1944) recorded this condition as rare in *T. t. orientalis*, and Godsil and Holmberg (1950) noted the same for *T. t. thynnus*. In all our material, including *T. maccoyii*, the artery passed between ribs 3 and 4, and divided between intermuscular bones 4 and 5 (between 5 and 6 in one specimen of *T. t. thynnus*).

The place of attachment of the internal wing of the pelvic girdle was said to be different in each of the three forms (Godsil and Holmberg, 1950). We found the condition in all three similar to their descriptions of *T. maccoyii*.

THUNNUS MACCOYII (Castelnau, 1872) SOUTHERN BLUEFIN TUNA

Thynnus maccoyii Castelnau, 1872: 104–105 (original description; Melbourne market).

Thunnus phillipsi Jordan and Evermann, 1926: 13 (original description; New Zealand), pl. 2, fig. 4.

Thunnus maccoyii, Jordan and Evermann, 1926: 13 (description). Serventy, 1941: 27–33 (description; Australia), fig. 5, pl. 2. Godsil and Holmberg, 1950 (comparison of Australian with New England and California specimens; anatomy). Mimura and Warashina, 1962. Iwai and Nakamura, 1964: 6, figs. 3E, F (olfactory rosettes). Iwai et al., 1965: 9 (synonymy), 33–34 (description), fig. 18. Nakamura, 1965: 18, figs. 3C, 5C, 7 (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Thunnus obesus, Fraser-Brunner, 1950: 144 (*T. maccoyii* in synonymy).

Thunnus thynnus maccoyii, Serventy, 1956a (counts, distribution around Australia). Munro, 1958: 111 (Australia). Robins, 1963 (biology; Australia).

Thunnus thynnus subspecies, Serventy, 1956a: 13 (probably a separate subspecies in S. Africa).

Thunnus thynnus orientalis, Jones and Silas, 1960: 381–382 (Indian Ocean), fig. 8. Collette and Gibbs, 1963: 28. Jones and Silas, 1963: 1788–1790 (Indian Ocean). Talbot and Penrith, 1963: 630–636 (description, biology; S. Africa). Jones and Silas, 1964: 30–34 (Indian Ocean).

Types of Nominal Species

Thynnus maccoyii Castelnau, 1872. No type specimens. Bauchot and Blanc (1961: 377) reported that a type specimen was catalogued in the collections of the Museum National d'Histoire Naturelle, Paris, in 1877, as number 515, but that the specimen cannot be located. Original description based on several specimens, fresh and dried, from the Melbourne, Australia, market, the largest 23 inches (585 mm.) long. This description is inadequate, but the short pectoral (two-thirds of head) suggests one of the bluefin tunas or *T. tonggol*, and the locality rules out all except *T. maccoyii* as now recognized.

Thunnus phillipsi Jordan and Evermann, 1926. Type originally designated as "A photograph, No. 596, Mus. Calif. Acad. Sci. . . . of a specimen taken in the Bay of Islands, New Zealand." This photograph is of a pug-headed mounted specimen in the Dominion Museum, Wellington. The cast is 1,575 mm. FL. The pectoral fin is short (295 mm.), which makes *T. maccoyii* the only reasonable assignment for this nominal species, *T. tonggol* not being known to occur in New Zealand. According to J. Moreland (pers. comm.), the pug-headedness appears to be the result of the fish being stood on its head forcing the processes of the premaxillaries up over the frontals where they remained when the cast was made.

Characters

Pectoral fin short, not more than 80 percent of head length, 20–23 percent of fork length in specimens 650–1,450 mm. (overlapping *T. tonggol;* slightly longer than *T. thynnus*). Caudal keels yellow in most specimens; this color possibly lost in larger adults.

Gill rakers 31–40, more numerous than in any other species of *Thunnus* except *T. thynnus*.

Liver with striations on ventral surface, its three lobes subequal in length, and with vascular cones on its dorsal side (as in *T. alalunga*, *T. obesus*, and *T. thynnus*). Spleen located on right side, and stomach on left (as in all except *T. alalunga*). Kidney with a very short "tail," reaching to the level of vertebra 8–12 (as in *T. thynnus*).

Cutaneous arteries originating at level of vertebra 4–5, passing laterally between ribs 2 and 3 or 3 and 4, and dividing between intermuscular bones 4 and 5 (as in *T. alalunga* and *T. thynnus*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. obesus* and *T. thynnus*). Post-cardinal vein absent (as in *T. alalunga* and *T. thynnus*).

Posterior parasphenoid margin forming an angle, becoming acute in large specimens (as in *T. alalunga*, *T. thynnus*, and, to a lesser degree, in *T. obesus*), occasionally rounded in small specimens. Alisphenoids extending far ventrad into orbital cavity; distance from most ventral part of alisphenoid to nearest point on parasphenoid goes into greatest height of anterior part of orbit two times or more (only *T. thynnus* and larger specimens of *T. tonggol* have a similar condition). Alisphenoids not known to fuse with parasphenoid as is the case in some *T. thynnus*. Subopercle relatively slender, its upper anterior margin usually almost vertical in its lower two-fifths or more, sloping posteriad in its upper portion (as in *T. thynnus*); rarely, there is no vertical portion.

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis on vertebra 9 (as in all except *T. thynnus* and *T. tonggol*). First closed haemal arch on vertebra 10 (as in *T. alalunga*, *T. thynnus*, and, rarely, all others except *T. tonggol*). Anterior haemal prezygapophyses arising high on haemal arch (as in *T. alalunga*, *T. thynnus*, and *T. obesus*). All haemal postzygapophyses short, less than half centrum length (as in *T. alalunga*, *T. thynnus*, and *T. obesus*). Ventrolateral foramina small, not more than one and one-half times width of haemal spine (as in *T. alalunga*, *T. thynnus*, and *T. obesus*).

Comparisons with *T. thynnus* are given in table 5.

Range

Thunnus maccoyii is apparently mainly restricted to the Southern Ocean, although it is impossible to evaluate many records. This species is best recognized at present by skeletal characters, although the yellow caudal keel is also diagnostic. We have examined skeletal material from Tasmanian waters reported by Godsil and Holmberg (1950); from western South Africa, reported by Talbot and Penrith (1963); additional specimens from the Sydney, Australia, market; from west of southern Australia; and from off the coast of Chile. The presence of *T. maccoyii* in the Pacific and Indian oceans off both sides of southern Australia and off Chile, and in the Atlantic off South Africa is thus definitely established. The geographic distribution summarized by Robins (1963) included waters north of New Zealand and areas off western Australia north almost to the Indonesian Islands. These records are probably correct, but need confirmation through osteological studies. Southeastern Pacific catches are reported by Japanese expeditions (Japan Fishery Agency, 1964). If these unconfirmed records are accepted, it seems likely that *T. maccoyii* will be found throughout the Southern Ocean south of 30° S.

THUNNUS THYNNUS (Linnaeus, 1758) BLUEFIN TUNA

The synonymy of each of the two subspecies is presented separately. The diagnosis of the species, discussion of nominal species and subspecies, and summary of the range consider both subspecies.

THUNNUS THYNNUS THYNNUS (Linnaeus, 1758) ATLANTIC BLUEFIN TUNA

Scomber pinnulis octo vel novem in extremo dorso ex sulco ad pinnas ventrales Artedi, 1738a: 31 (description) and 1738b: 141–142 (references to Aristotle, Ovid, Pliny, etc.).

Scomber thynnus Linnaeus, 1758: 297–298 (original description; based on Artedi, 1738). Bonnaterre, 1788: 139, pl. 58, fig. 228. Gmelin, 1789: 1330–1331 (description, synonymy). Lacépède, 1800: 598, 605–632 (description, synonymy). Risso, 1810: 163 (Nice).

Thynnus thynnus, Cuvier, 1817: 313 (Mediterranean). Günther, 1860: 362–363 (synonymy, description; Atlantic and Mediterranean).

Thynnus mediterraneus Risso, 1826: 414–415 (substitute name for *Scomber thynnus* Linnaeus, 1758; Nice).

Thynnus vulgaris Cuvier *in* Cuvier and Valenciennes, 1831: 42–71 (substitution of new name for *Scomber thynnus* Linnaeus, 1758), pl. 210.

Thunnus vulgaris, South, 1845: 620–621 (description, natural history).

Thynnus secundo-dorsalis Storer, 1967: 65–67 (original description; Massachusetts Bay), pl. 12, fig. 4.

Orcynus thynnus, Poey, 1875: 144–145. Lütken, 1880: 460–464, 595–596 (in part; development). Buen, 1925 (migrations, biology; E. Atlantic).

Orcynus secondidorsalis, Poey, 1875: 145 (Cuba).

Albacora thynnus, Jordan, 1888. Dresslar and Fesler, 1889: 439–440 (synonymy in part), pl. 7.

Thunnus thynnus, Jordan and Evermann, 1896: 870 (description, synonymy in part; a single worldwide species of bluefin). Meek and Hildebrand, 1923: 314–315 (description, synonymy in part). Jordan and Evermann, 1926: 10 (synonymy; Europe). Barnard, 1927: 798–799 (S. Africa). Buen, 1930: 49 (synonymy), fig. 7. Frade, 1931b (biometrics; Portugal). Frade, 1931c (meristics; E. Atlantic). Crane, 1936 (description; Gulf of Maine). Fowler, 1936: 619–620 (synonymy, description). Tortonese, 1939: 324 (Yokohama). Bellón and Bardán de Bellón, 1949: 8–11 (Canary Is.). Smith, 1949, 1953: 298 (S. Africa), pl. 66, fig. 831. Godsil and Holmberg, 1950 (anatomy; New England). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 143 (synonymy in part), fig. 4. Rivas, 1951: 217–219 (description, synonymy). Ginsburg, 1953: 1 (the name *thynnus* restricted to the E. Atlantic population of bluefin). Morice, 1953: 67–68, figs. 1, 2 (liver; E. Atlantic). Bellón, 1954 (description, relationships, biology, anatomy, distribution). Mather and Day, 1954: 181 (W. Atlantic). Rivas, 1954b: 302–322 (spawning in straits of Florida), figs. 1–3. Rivas, 1955 (comparison between Gulf of Maine and Florida specimens). de Sylva, 1955: 33–40 (osteology, relationships), fig. 55 (neurocranium). Bullis and Mather, 1956 (key to Caribbean species of *Thunnus*). Robins, 1957 (counts on dorsal and anal fins, gill rakers; one species of bluefin in the Atlantic). Mather and Schuck, 1960 (growth; NW. Atlantic). Frade and Vilela, 1962: 17–58 (morphology, biology; E. Atlantic). Tiews, 1963 (biology; Atlantic.)

Thunnus secundodorsalis, Jordan and Evermann, 1926: 12 (description). Jordan et al., 1930: 260. Ginsburg, 1953: 1–3 (W. Atlantic; summary of meristics from various authors).

Thunnus thynnus thynnus, Serventy, 1956a: 11–13 (subspecies found along Atlantic coast of Europe). Talbot and Penrith, 1963: 633–640 (description, biology; S. Africa).

Thunnus thynnus coretta, Serventy, 1956a: 11–13 (subspecies found along Atlantic coast of America).

Misidentification

Thynnus brachypterus Cuvier (1829) was based on illustrations by Rondelet (1554) and Duhamel du Monceau (1769). Collette (1966) has indicated that this name is a synonym of *Sarda sarda* (Bloch). Although Cuvier (*in* Cuvier and Valenciennes, 1831) based his later description of *T. brachypterus* on specimens, four of which are *T. thynnus* and one *Euthynnus alletteratus*, this can not be regarded as the original description, and these specimens are not types.

Types of Nominal Species

Scomber thynnus Linnaeus, 1758. No type specimens. Original description not diagnostic, but based on Artedi (1738a, p. 31), who stated: "Longitude 7 pedum circiter." This could only refer to the bluefin tuna.

Thynnus mediterraneus Risso, 1826. Substitute name for *Scomber thynnus* Linnaeus, 1758, and taking the same type.

Thynnus vulgaris Cuvier *in* Cuvier and Valenciennes, 1831. Substitute name for *Scomber thynnus* Linnaeus, 1758, and taking the same type.

Thynnus secundodorsalis Storer, 1867. No type specimens. Original description based on two specimens, 8 feet, 6 inches (1,590 mm.) and 9 feet, 3 inches (1,820 mm.) total length. The pectorals "about one seventh of length of fish," the size and the locality (Mass.) unquestionably assign this nominal species to the synonymy of *Thunnus thynnus thynnus*.

THUNNUS THYNNUS ORIENTALIS
(Temminck and Schlegel, 1844)
PACIFIC BLUEFIN TUNA

Thynnus orientalis Temminck and Schlegel, 1844: 94–95 (original description; Japan). Günther, 1860: 362 (in footnote as dubious species).

Orcynus schlegelii Steindachner *in* Steindachner and Döderlein, 1884: 10–11 (original description; Tokyo), pl. 3, fig. 1.

Thunnus thynnus, Jordan and Evermann, 1896: 870 (description and synonymy in part). Jordan et al., 1913: 121 (Japan). Walford, 1937: 7–13 (description; Pacific specimens; possibility of a single worldwide species of bluefin), color pl. 34.

Brock, 1938 (Washington). Godsil and Byers, 1944: 88–102 (anatomy; E. Pacific), figs. 48–58. Tinker, 1944: 151 (Hawaii), pl. 1, fig. 8. Brock, 1949: 276 (key to Hawaiian tunas). Fraser-Brunner, 1950: 142–143 (synonymy in part), fig. 4. Godsil and Holmberg, 1950 (anatomy; California). June, 1952a (Hawaii). Buen, 1953 (Chile; but might be *T. maccoyii*). Iwai and Nakamura, 1964: 6, figs. 3C, D (olfactory rosettes). Iwai et al., 1965: 3, 6–8 (synonymy), 31–33 (description), fig. 16. Nakamura, 1965: 17–18, figs. 3B, 5B, 6 (osteology). Nakamura and Warashina, 1965: 9–10 (E. Indian and SE. Pacific oceans). Nakamura and Kikawa, 1966 (infracentral grooves).

Orcynus thynnus, Kitahara, 1897: 1 (description; Japan), pl. 1, fig. 1.

Thunnus schlegelii, Jordan and Snyder, 1900: 352 (Tokyo). Jordan and Snyder, 1901: 64 (Yokohama).

Thunnus orientalis, Kishinouye, 1915: 17 (description, anatomy; Japan), pl. 1, fig. 9. Kishinouye, 1923: 437–442 (anatomy; Japan), figs. 3, 21, 43, 44, 50. Jordan and Hubbs, 1925: 216–217 (Japan). Jordan and Evermann, 1926: 14 (description). Tinker, 1944: 157–158 (Hawaii). Brock, 1949: 276 (key to Hawaiian tunas). Gosline and Brock, 1960: 259 (description; Hawaii), 336 (synonymy), fig. 257h. Yamanaka et al., 1963 (biology; Japan).

Thunnus saliens Jordan and Evermann, 1926: 10–11 (original description; California), pls. 1–2, figs. 1–3. Jordan et al., 1930: 259. Ginsburg, 1953: 3 (*saliens* recognized as American Pacific species of bluefin). Neave, 1959 (N. end Vancouver Is.). Bell, 1963 (biology; E. Pacific).

Thunnus thynnus orientalis, Serventy, 1956a: 11–13 (the subspecies found along Asiatic coast of N. Pacific).

Thunnus thynnus saliens, Serventy, 1956a: 11–13 (the subspecies found along Pacific coast of N. America). Buen, 1958: 24–25 (Chile; but might be *T. maccoyii*).

Types of Nominal Species

Thynnus orientalis Temminck and Schlegel, 1844. Holotype RMNH 794, 450 mm. fork length, a mounted specimen from Japan with a pectoral fin 18.4 percent of fork length.

Orcynus schlegelii Steindachner, 1884. Holotype (not seen by us) presumably in Vienna Museum, 360 mm. fork length. The pectoral of barely more than half the head length and the locality (Japan) enable referral of this nominal species to the synonymy of *T. thynnus orientalis* (Temminck and Schlegel, 1844).

Thunnus saliens Jordan and Evermann, 1926. Type originally designated as "No. 595, Mus. Calif. Acad. Sci., a photograph of a specimen weighing 157½ pounds taken . . . off Catalina, California." The photograph is clearly of a tuna with short pectoral fins; Jordan and Evermann (1926) recorded the fin length as 5½ (p. 9) or 5 (p. 10) in (standard) length, or about 20 percent. The locality allows referral to the synonymy of *T. thynnus orientalis*.

Characters

Pectoral fin short, not more than 80 percent of head length, less than 23 percent of fork length, slightly shorter than in *T. maccoyii* at a given size (fig. 33), overlapped by *T. tonggol*.

Gill rakers 34–43 in *T. t. thynnus*, 32–40 in *T. t. orientalis*, more numerous than in any other species of *Thunnus* except *T. maccoyii*.

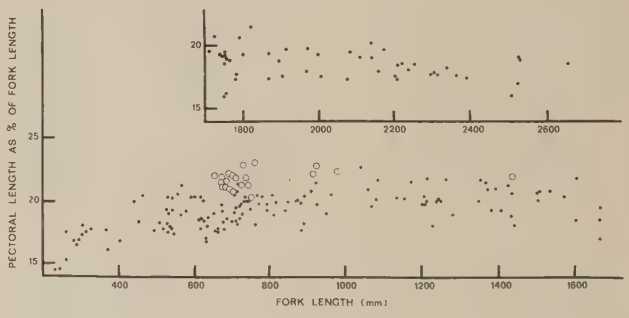


FIGURE 33.—Relative length of pectoral fin in *Thunnus thynnus* (dots) and *T. maccoyii* (open circles).

Liver with striations on ventral surface, its three lobes subequal in length, and with vascular cones on its dorsal side (as in *T. alalunga*, *T. obesus*, and *T. maccoyii*). Spleen located on right side, stomach on left (as in all except *T. alalunga*). Kidney with a very short tail, reaching to level of vertebra 8–11 (as in *T. maccoyii*).

Cutaneous arteries originating at level of vertebra 3–6 (usually 4 or 5), passing laterally between ribs 3 and 4 (occasionally 2 and 3) and dividing between intermuscular bones 4 and 5 or 5 and 6 (as in *T. alalunga* and *T. maccoyii*). Two rows of arterioles and venules arising from each main lateral cutaneous branch (as in *T. obesus* and *T. maccoyii*). Post-

cardinal vein absent (as in *T. alalunga* and *T. maccoyii*).

Posterior parasphenoid margin forming an angle, becoming acute in large specimens (as in *T. alalunga*, *T. maccoyii*, and, to a lesser degree, in *T. obesus*), occasionally rounded in small specimens. Alisphenoids extending far ventrad into orbital cavity; distance from most ventral part of alisphenoid to nearest point on parasphenoid goes into greatest height of anterior part of orbit two times or more (only *T. maccoyii* and larger specimens of *T. tonggol* have a similar condition). Alisphenoids fused to parasphenoid in some larger specimens. Subopercle (see fig. 9) relatively slender, its upper anterior margin usually almost vertical in its lower two-fifths or more, sloping posteriad in its upper portion (as in *T. maccoyii*); rarely there is no vertical portion.

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis on vertebra 8. First closed haemal arch usually on vertebra 10 (as in *T. alalunga* and *T. maccoyii*), sometimes on 11 (as in the other five species). Anterior haemal prezygapophyses arising high on haemal arch (as in *T. maccoyii* and *T. obesus*). All haemal postzygapophyses short, less than half the centrum length (as in *T. maccoyii* and *T. obesus*). Ventrolateral foramina small, not more than one and one-half times width of haemal spine (as in *T. alalunga*, *T. maccoyii*, and *T. obesus*).

Comparisons with *T. maccoyii* are given in table 5.

Range

T. thynnus thynnus has been found in the western Atlantic from Hamilton Inlet, Labrador (La Monte, 1946: 22), and Newfoundland, south along the Atlantic coast of the United States into the Gulf of Mexico and Caribbean Sea (Wathne, 1959). It is known off Venezuela (Fernandez-Yepez and Santaella, 1956), and south to northeastern Brazil. In the eastern Atlantic, *T. t. thynnus* is found from the Lofoten Islands of Norway (about 70° N.), south along the coast of Europe and north Africa, south to the Canary Islands. Records from near Cape Verde Islands, Angola, and Republic of South Africa have been questioned (Tiews, 1963), but gill-raker counts given by Talbot and Penrith (1963) for large specimens caught from January to March suggest convincingly that *T. t. thynnus* does occur west of the Cape Peninsula of South Africa, and we have examined one specimen from there.

Tag returns have shown that there is at least some interchange between eastern and western North Atlantic *T. t. thynnus*. Mather (1960) reported two specimens tagged off Martha's Vineyard, Mass., and recaptured in the Bay of Biscay 2 to 5 years later. Two large specimens tagged off Cat Cay, Bahamas, were recaptured off Bergen, Norway, a distance of over 4,000 miles, after 118 and 119 days at large (Mather, 1962).

T. thynnus orientalis has been reported in the eastern north Pacific from the Shelikof Straits, north of Kodiak Island, in the Gulf of Alaska (Radovich, 1961), off Vancouver Island (Neave, 1959), off Willapa Bay and the mouth of the Columbia River (Brock, 1938), regularly off southern California and the length of Baja Calif. (Bell, 1963). In the western north Pacific, *T. t. orientalis* is known from the island of Sakhalin in the southern Okhotsk Sea, southward on both sides of Japan, to the northern Philippines; eastward from Japan between about 30°–40° N. to about 160° W.; and eastward between about 5°–10° N. from about 135°–175° E. (Yamanaka et al., 1963). It is taken occasionally in Hawaiian waters (Jordan and Jordan, 1922; Fowler, 1928; June, 1952a).

The contention that both eastern and western north Pacific *T. thynnus* constitute a single subspecies is supported by the recapture off Japan of at least three specimens that had been tagged 2 to 5 years previously near Guadalupe Island, Mexico (Orange and Fink, 1963; Anonymous, 1964).

Thunnus thynnus has been recorded from the Galapagos area (Snodgrass and Heller, 1905; Herre, 1936), but there is no supporting evidence which would eliminate *T. maccoyii* or any other species from consideration.

Nakamura and Warashina (1965) reported *T. thynnus orientalis* (as *T. thynnus*) from two areas previously not verified. Two specimens, 2,657 mm. and 2,200 mm., were taken in the Indian Ocean off western Australia at 28°24′ S., 105°56′ E. and 27°43′ S., 102°25′ E., respectively. Another, 2,206 mm., was captured in the southeastern Pacific at about 37°11′ S., 114°41′ W. Specimens from Chile had previously been reported by Buen (1953, 1958), as *T. thynnus saliens*. These are areas from which *T. maccoyii* is known. Nakamura and Warashina gave measurements of one specimen from each locality. Converting their figures for pectoral length into percent of fork length (their "total length") gives 18.6 and 17.5 percent, falling below our data for smaller *T. maccoyii* and agreeing well with *T.*

thynnus orientalis (table 5). All three, however, are much larger than the largest reliably identified *T. maccoyii* (1,748 mm.; Iwai and Nakamura, 1964b: 2). It is entirely possible that the two best external diagnostic characters—color of caudal keel and length of pectoral fin—may no longer be distinct at large sizes. At the present time only examination of vertebral characters can offer assurance of their identity.

We examined the skull and vertebral column of the specimen from 37°11′ S., 114°41′ W. The skull (290 mm.) is larger than any we have examined of *T. maccoyii* and has the alisphenoids fused to the parasphenoids, a condition we have found only in large specimens of *T. thynnus*. The first ventrally directed parapophyses are on the eighth vertebra and the first closed haemal arch is on the tenth vertebra as in *T. thynnus*. Three other vertebral characters useful in distinguishing *T. thynnus* from *T. maccoyii* have the following values: 9th vertebra: parapophysis height divided by least distance apart —4.2; 10th vertebra: canal height divided by least width of processes—2.9; and 10th vertebra: canal height divided by canal width—1.8. The first and third are higher and the second is well below the range we have found for *T. maccoyii*, and all agree well with our data for *T. t. orientalis* (table 5). Unfortunately, skeletons of the suspect Indian Ocean specimens are not available, but specimens from this region, observed by us in the Yaizu market, appeared to have the dorsal bulge of the body cavity as in *T. thynnus*.

THUNNUS TONGGOL (Bleeker, 1851) LONGTAIL TUNA

Thynnus tonggol Bleeker, 1851: 356–357 (original description; Batavia Sea). Günther, 1860: 364.

Thunnus rarus Kishinouye, 1915: 28 (original description; Tokyo market), pl. 1, fig. 13.

Neothunnus rarus, Kishinouye, 1923: 448–450 (anatomy), figs. 24–48, 64. Herre, 1940: 39 (Malaya). Nichols and La Monte, 1941: 32 (synonymy in part).

Kishinoella rara, Jordan and Hubbs, 1925: 219 (placed in the new genus *Kishinoella*). Jordan and Evermann, 1926: 26 (description). Herre, 1945: 148 (Zamboanga, Philippines).

Neothunnus tonggol, Jordan and Evermann, 1926: 22.

Thunnus nicolsoni Whitley, 1936: 30–31 (original description; Queensland), fig. 2.

Thunnus tonggol, Tortonese, 1939: 326 (Java Sea). Fraser-Brunner, 1950: 142 (key to *Thunnus*), 145–146 (synonymy), fig. 8. de Beaufort, 1951: 225–226 (synonymy; description; Bleeker's types checked). Iwai and Nakamura, 1964: 6, fig. 31 (olfactory rosettes). Jones and Silas, 1964: 38–40 (Indian Ocean). Iwai et al., 1965: 16–17 (synonymy), 39–40 (description), fig. 23. Nakamura, 1965: 24, figs. 3G, 12, 13A (osteology). Nakamura and Kikawa, 1966 (infracentral grooves).

Kishinoella tonggol, Serventy, 1941: 33–38 (description; Australia), figs. 6–9, pl. 2. Serventy, 1942 (description, anatomy, synonymy; Australia), fig. 1, pls. 3–5. Serventy, 1956b (counts, distribution; Australia). Munro, 1958: 111 (Australia.) Jones and Silas, 1960: 384–385 (west coast of India), fig. 11. Ranade, 1961 (description; Arabian Sea). Jones, 1963 (biology; Indian Ocean). Jones and Silas, 1963: 1792–1793 (Indian Ocean).

Misidentifications

Munro (1957) reported a specimen of tuna as *Parathunnus mebachi* from southern Queensland. Rivas (1961) considered this specimen to be the same as his *T. argentivittatus*, but as we have shown under the account of *T. albacares*, Rivas' account and that of Schaefer and Walford (1950) is based on a specimen of *T. tonggol*. Judging from the low number of gill rakers (7+16=23), pectoral length, and distance from snout to second dorsal origin reported by Munro (1957), his specimen was also *T. tonggol*. His later account (Munro, 1958) confirms this opinion. Serventy (1942, 1956b), Fraser-Brunner (1950), and others have considered *Kishinoella zacalles* Jordan and Evermann (1926) as close to or a synonym of *T. tonggol*, but *zacalles* is a synonym of *T. albacares*, as we show under the account of that species.

Types of Nominal Species

Thynnus tonggol Bleeker, 1851. No type specimens known to us. The designation of a neotype by Boeseman (1964) was not in accordance with the International Code of Zoological Nomenclature (1964, Article 75), which states, among other things, that a neotype is to be designated only in connection with revisionary work, and that the designator of a neotype must give his reasons for believing all original type material to be lost or destroyed and the steps that have been taken to trace it. Since designation of a neotype would solve no nomenclatorial problems, and since we have not exhaustively sought

type material, we do not deem it necessary or proper to take this action ourselves.

Bleeker's original description was based on a single specimen, 650 mm. long, from "Batavia, in mari," with a pectoral fin shorter than the head and no swimbladder. The description obviously applies to the species for which the name is now used.

Thunnus rarus Kishinouye, 1915. No type specimens. Original description based on a single specimen, 28.8 inches (ca. 730 mm.) long, from Nagasaki. The gill-raker count of 6+17, short pectoral fins (no measurements given), and lack of swimbladder show this nominal species to be a synonym of *T. tonggol.*

Thunnus nicolsoni Whitley, 1936. Holotype Australian Museum IA. 6553, a 189 mm. head of a specimen originally 30 inches (762 mm.) total length caught between Lindeman and Maher Islands, Cumberland Group, North Queensland, Australia. The gill raker count of 6+16 and pectoral shorter than head establish this as a synonym of *T. tonggol.*

Characters

Pectoral fin (see fig. 26) varying in length from medium (22–31 percent of fork length) in specimens less than 600 mm. to short (16–22 percent) in those over 600 mm. (the latter resembling only *T. thynnus* and *T. maccoyii*). Tail region comparatively long, longest in large specimens; distance from snout to second dorsal origin 49–55 percent of fork length, decreasing with size (consistently lower than in any other *Thunnus* species).

Gill rakers 19–26 (rarely to 28), fewer than in any other *Thunnus* species except *T. atlanticus.*

Liver without striations on ventral surface, its right lobe long and narrow, without vascular cones on its dorsal side (as in *T. albacares* and *T. atlanticus*). Spleen on right side, stomach on left (as in all except *T. alalunga*). Kidney with a bulky anterior mass and a long, narrow tail, reaching vertebra 15–17.

Swimbladder absent or rudimentary.

Cutaneous arteries originating at the level of vertebra 7–8, passing laterally between ribs 4 and 5 or 5 and 6, dividing between intermuscular bones 6 and 7 (as in *T. albacares, T. obesus,* and *T. atlanticus*). A single row of arterioles and venules arising from each cutaneous branch (as in *T. alalunga, T. albacares,* and *T. atlanticus*), but arising from the lateral side of each vessel (as in *T. albacares* and *T. atlanticus*).

Post-cardinal vein present (as in *T. albacares, T. atlanticus,* and *T. obesus*).

Posterior parasphenoid margin not angulate (similar to *T. albacares* and *T. atlanticus*).

Vertebrae 18+21 (as in all except *T. atlanticus*). First ventrally directed parapophysis usually on vertebra 10. First closed haemal arch usually on vertebra 11 (as in *T. atlanticus, T. albacares, T. obesus,* occasionally *T. thynnus*) or 12. Anterior haemal prezygapophyses arising well ventrad on haemal spines (as in *T. albacares* and *T. atlanticus*). Haemal postzygapophyses long, the longest about equal to or longer than centrum length (as in *T. atlanticus,* slightly longer than in *T. albacares*). Anteriormost ventrolateral foramina large, more than three times as wide as haemal spine (as in *T. albacares* and *T. atlanticus*).

Nominal Species

There appear to be only two synonyms of *T. tonggol: Thunnus rarus* Kishinouye from Japan and *T. nicolsoni* Whitley from Queensland. Rivas (1961) placed *T. nicolsoni* in the synonymy of *T. albacares* but the gill raker count of 6+16=22 alone (Whitley, 1936) is enough to show that this is incorrect.

Range

T. tonggol is limited to the Indo-West Pacific. It is found from the western and southern coasts of Kyushyu and the southwestern part of the Japan Sea (Kishinouye, 1923, p. 449), south through the Batavia Sea (Bleeker, 1851, p. 356) to New Guinea, New Britain, and the entire north coast of Australia (Serventy, 1956b). On the Australian east coast, it is reported at least as far south as Twofold Bay, New South Wales; on the west coast it reaches at least to Cockburn Sound in the Freemantle area. Its range in the Indian Ocean (Jones, 1963) includes the Indo-Australian Archipelago, Andaman Islands, both coasts of India, southern Arabia, the Somalia coast, and the Red Sea, but it was not reported from East African waters by Williams (1964) or Merrett and Thorp (1966).

Gill-raker counts indicate differences between populations in the western Indian Ocean, with a modal number of 26, and those in the eastern Indian Ocean and western Pacific, with a mode of 23. More data are necessary to corroborate this.

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APPENDIX

Figure A-1.—Lateral view of skulls of *Thunnus* species. (top) *T. atlanticus*, skull length 88 mm.; (middle) *T. tonggol*, 56 mm.; (bottom) *T. tonggol*, 122 mm.

FIGURE A-2.—Lateral view of skulls of *Thunnus* species. (top) *T. alalunga*, skull length 151 mm.; (middle) *T. thynnus*, 103 mm.; (bottom) *T. thynnus*, 335 mm.

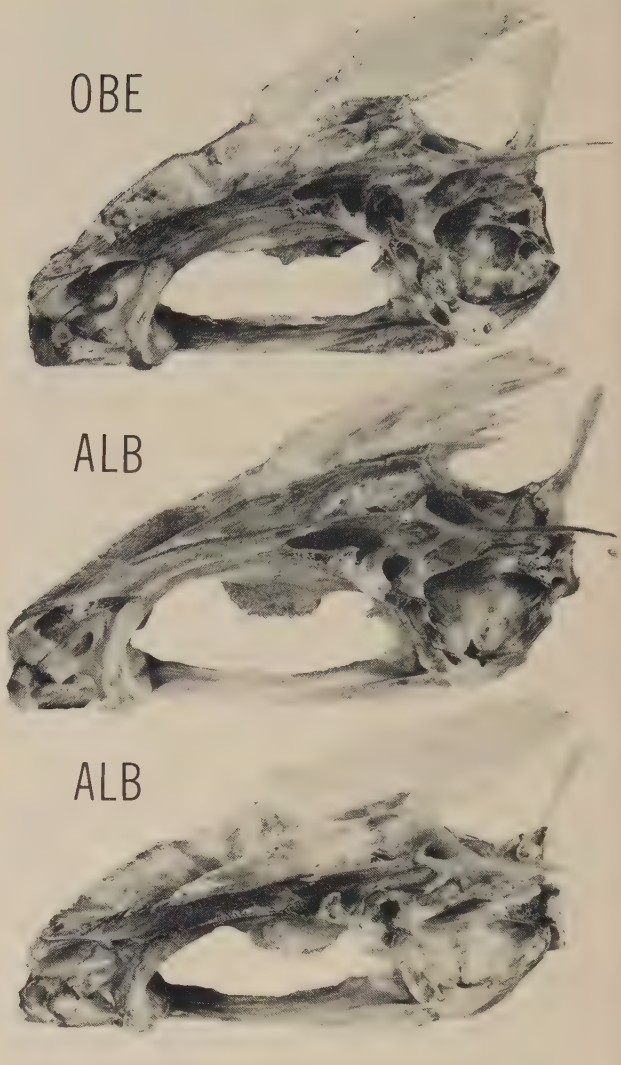

FIGURE A-3.—Lateral view of skulls of *Thunnus* species. (top) *T. obesus*, skull length 200 mm.; (middle) *T. albacares*, 113 mm.; (bottom) *T. albacares*, 164 mm.

INFLUENCE OF ROCKY REACH DAM AND THE TEMPERATURE OF THE OKANOGAN RIVER ON THE UPSTREAM MIGRATION OF SOCKEYE SALMON

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ABSTRACT

Tagging experiments show that Rocky Reach Dam, constructed on the Columbia River 7 miles above Wenatchee, Wash., in 1957–61, has not appreciably increased the time required for adult sockeye salmon (*Oncorhynchus nerka*) to migrate to Zosel Dam on the Okanogan River (a tributary to the Columbia River above Rocky Reach Dam). Water temperature of the Okanogan River is, however, a major cause of delay. Above 70° F., rising or stable Okanogan River temperatures block the entry of the fish from the Columbia River into the Okanogan River; falling temperatures allow the migration to resume. Below 70° F., migration is not blocked by rising or stable temperatures. Delay may reduce survival because it increases the exposure of the sockeye salmon to other factors that affect them adversely.

INTRODUCTION

If Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) are to reproduce successfully, sufficient adults in spawning condition must reach the spawning grounds. Consequences can be serious if the migrants are delayed en route. Thompson (1945) showed, for example, that of the tagged sockeye salmon (*Oncorhynchus nerka*) that had been delayed longer than 12 days at the Hell's Gate rock slide on the Fraser River, British Columbia, in 1941, practically none reached their spawning grounds. He also suggested that lesser delays reduced the reproductive capacity of the fish.

Although they are equipped with facilities for passing fish, hydroelectric dams on the migration routes constitute another type of barrier which can delay adults en route to their upstream spawning grounds. To assess and find ways to minimize the effects of these dams as they are built on the Columbia River is a most important aim of the agencies concerned with the salmon and steelhead resources of the stream. One facet of this work is to detect and minimize any delay of the adults as they migrate upstream. The time required for adults to locate and ascend fish ladders is sometimes reduced, for example, by altering the spill pattern to improve attraction to the ladders or even by modifying the ladders themselves.

In this paper we show that Rocky Reach Dam, constructed on the Columbia River, 7 miles above Wenatchee, Wash., in 1957–61, has not appreciably increased the time required for sockeye salmon to migrate from Rock Island Dam (below Rocky Reach Dam) to Zosel Dam on the Okanogan River, a tributary to the Columbia River above Rocky Reach Dam (fig. 1). We also illustrate how the temperature of the Okanogan River periodically blocks the upstream migration of the sockeye salmon at the confluence of the Okanogan and Columbia Rivers.

This study originated as part of a broad program to assess the effects of Rocky Reach Dam on the fish and wildlife resources of the upper Columbia River. The program was developed by representatives of interested State and Federal agencies and financed by Public Utility District Number 1 of Chelan

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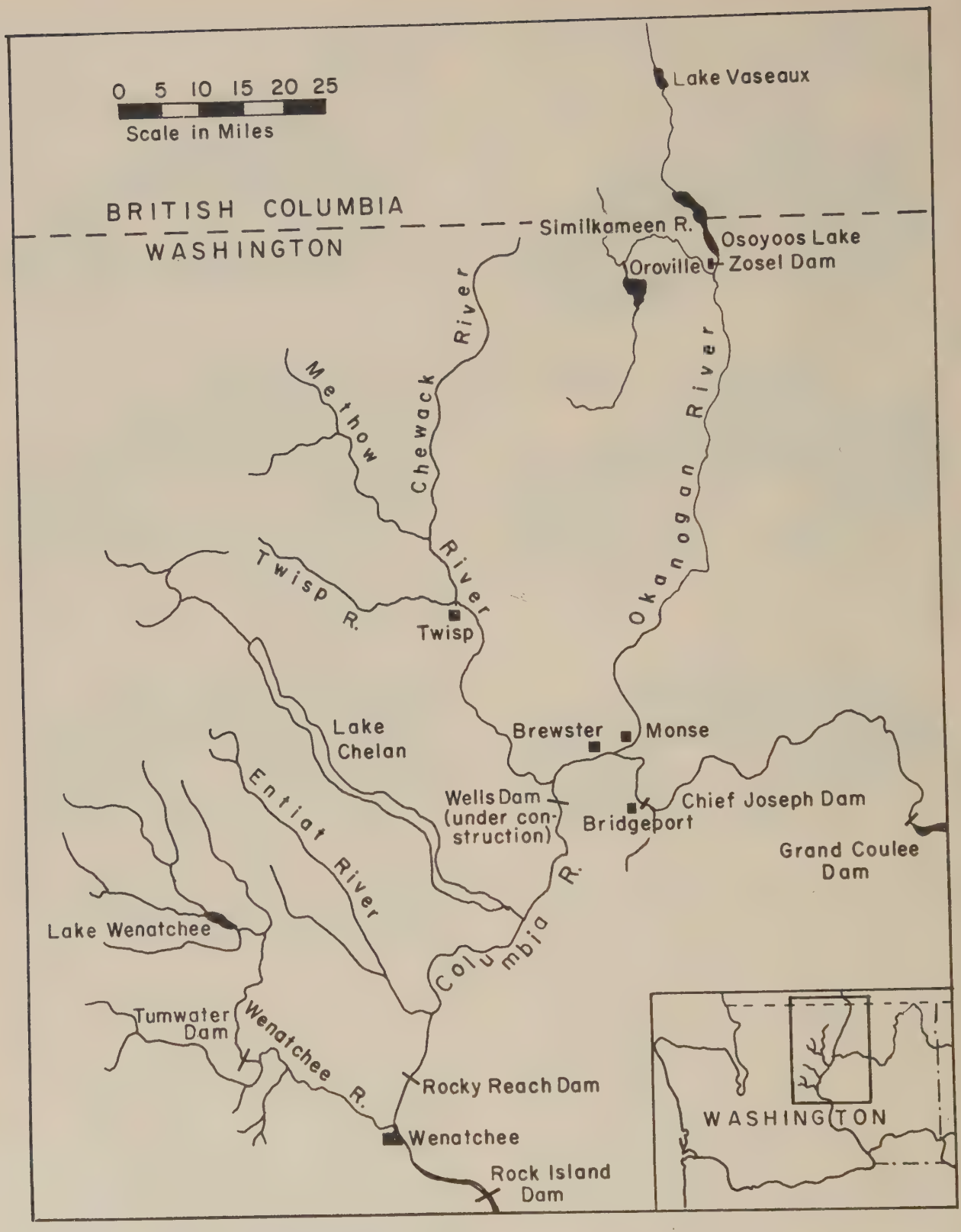

FIGURE 1.—The Columbia River and the locations important to the present study.

County, the builders of Rocky Reach Dam, in accordance with the terms of Federal Power Commission license number 2145. Biologists of the Bureau of Commercial Fisheries were designated to study possible delay because of their experience with a similar investigation at Rock Island Dam in 1953–56 (French and Wahle, 1966).

The study underwent a major expansion as it proceeded. Originally, the sole aim was to measure delay, if any, caused to upstream-migrating adult salmonids by Rocky Reach Dam. This aim was to be accomplished by comparing the time required for tagged sockeye salmon to migrate from the forebay (reservoir) of Rock Island Dam to Zosel Dam, before (1957) and after (1962 and 1963) the completion of Rocky Reach Dam. If minimal influence by other factors were assumed, any major change in travel time could be attributed to the new structure.

French and Wahle (1960) summarized the "predam" work (performed before the dam was built). Because too few tagged fish were observed at Zosel Dam in 1957, they estimated the travel time (10.7 days) from tagged sockeye salmon that had been released in the Rock Island Dam forebay and later observed at Zosel Dam during the earlier (1953–56) study.

The tagging results in the first "postdam" year (1962) had a profound impact on our investigation. Sockeye salmon migrating through the study area were noticeably delayed—apparently by high water temperatures of the Okanogan River. If a temperature block were shown to exist, the assumption of minimal influence by factors other than Rocky Reach Dam would have been invalidated and the straightforward comparison of "predam" and "postdam" travel times as a measure of delay ruled out —unless the influence of the various factors could be examined separately. It was necessary, therefore, to confirm the existence of the temperature block, to reexamine the estimated "predam" travel time, and finally to evaluate Okanogan River temperatures as well as Rocky Reach Dam as sources of delay to sockeye salmon in their upstream migration. These expanded objectives greatly increased the complexity of the "postdam" phase of the study.

METHODS AND MATERIALS

The experimental procedure was as follows: (1) determine, both before and after the completion of Rocky Reach Dam, the time required for tagged sockeye salmon to migrate from the Rock Island forebay to Zosel Dam; (2) determine the time required for tagged sockeye salmon to migrate from the Rock Island forebay to Rocky Reach Dam; (3) examine the variability in passage time in relation to Rocky Reach Dam and the flows and temperatures of the Okanogan and Columbia Rivers.

Tagging experiments provided the answers to items (1) and (2). For item (3), these same tagging data were supplemented by counts of sockeye salmon made at Rock Island and Zosel Dams in years when there was no tagging.

SOCKEYE SALMON AS THE STUDY SPECIES

Observations were confined to sockeye, the only salmon that can be intercepted in significant numbers above Rocky Reach Dam while still actively migrating to the spawning grounds.

Most sockeye salmon that pass Rock Island Dam are bound for spawning areas in the Wenatchee and Okanogan River systems. Those that pass Rocky Reach Dam are, on the other hand, mostly Okanogan-bound fish, because the Wenatchee population leaves the main Columbia River below Rocky Reach Dam. After sockeye salmon pass Rocky Reach Dam, they move to the mouth of the Okanogan River near Brewster, Wash., and continue up the Okanogan into Lake Osoyoos, where they remain until they migrate to the spawning grounds, 10 to 15 miles above the lake, in late September. We have assumed that the Okanogan and Wenatchee populations pass Rock Island Dam simultaneously. The close similarity in the shapes of the graphs of sockeye salmon counts for Rock Island and Rocky Reach Dams (examples of which are shown in figure 10, in conjunction with other data) suggests that this assumption is reasonable.

TAGGING

Sockeye salmon were tagged at Rock Island Dam in 1953–57, before Rocky Reach Dam was constructed, and in 1962 and 1963, after construction. The numbers of tagged sockeye salmon that were later observed at Zosel Dam in 1953, 1954, 1962, and 1963 are presented in table 1. The effort to observe tagged sockeye salmon at Zosel Dam was so variable and so ineffective in 1955–57 (for reasons given later) that data for these years are not included.

The tagging procedure was the same each year. Tagging was started when the daily count reached about one thousand fish and continued until it dropped to about one thousand near the end of the

TABLE 1.—*Number of sockeye salmon tagged at Rock Island Dam and observed at Zosel Dam in 1953, 1954, 1962 and 1963*

Year	Tagged at Rock Island Dam	Observed at Zosel Dam
	Number	*Number*
1953	710	334
1954	1,234	215
1962	1,009	89
1963	730	193

run. In 1954 and 1963, tagging was continued for periods of 2 to 4 consecutive days, separated by intervening 3 to 4 day periods of no tagging. Tagging was all at the end of the run in 1953 and was confined to the middle portion of the small run in 1962.

The method of tagging was standard for these studies. Fish were trapped at Rock Island Dam in either the fishway or forebay (figs. 2 and 3), transported by tank truck to the release sites, tagged, and released. Tagging time seldom exceeded 30 seconds per fish.

Several types and colors of tags were used. Petersen plastic disks were used alone in 1962 and 1963, but were used in combination with plastic bars and vinyl streamers in 1953 and 1954. Nickel pins, inserted through the body just below the dorsal fin, provided the attachment. Tags were always applied in pairs, so that the same color and type of tag showed on both sides of the fish.

STATIONS FOR COUNTING SOCKEYE SALMON AND OBSERVING TAGS

Zosel Dam, which lies on the Okanogan River at Oroville, Wash., 1 mile below Lake Osoyoos, is the principal upstream location for the observation of tagged fish. The dam, which forms a sawmill pond, is provided with two fishways, each with a trap at its exit for the capture of upstream-migrating fish. Sockeye salmon were counted at Zosel Dam in 1935–37, 1944, 1952–57, 1962, and 1963. Since the dam was modified in 1948, however, fish have been able to pass upstream at certain water levels without using the fishways. When stream flow exceeds the

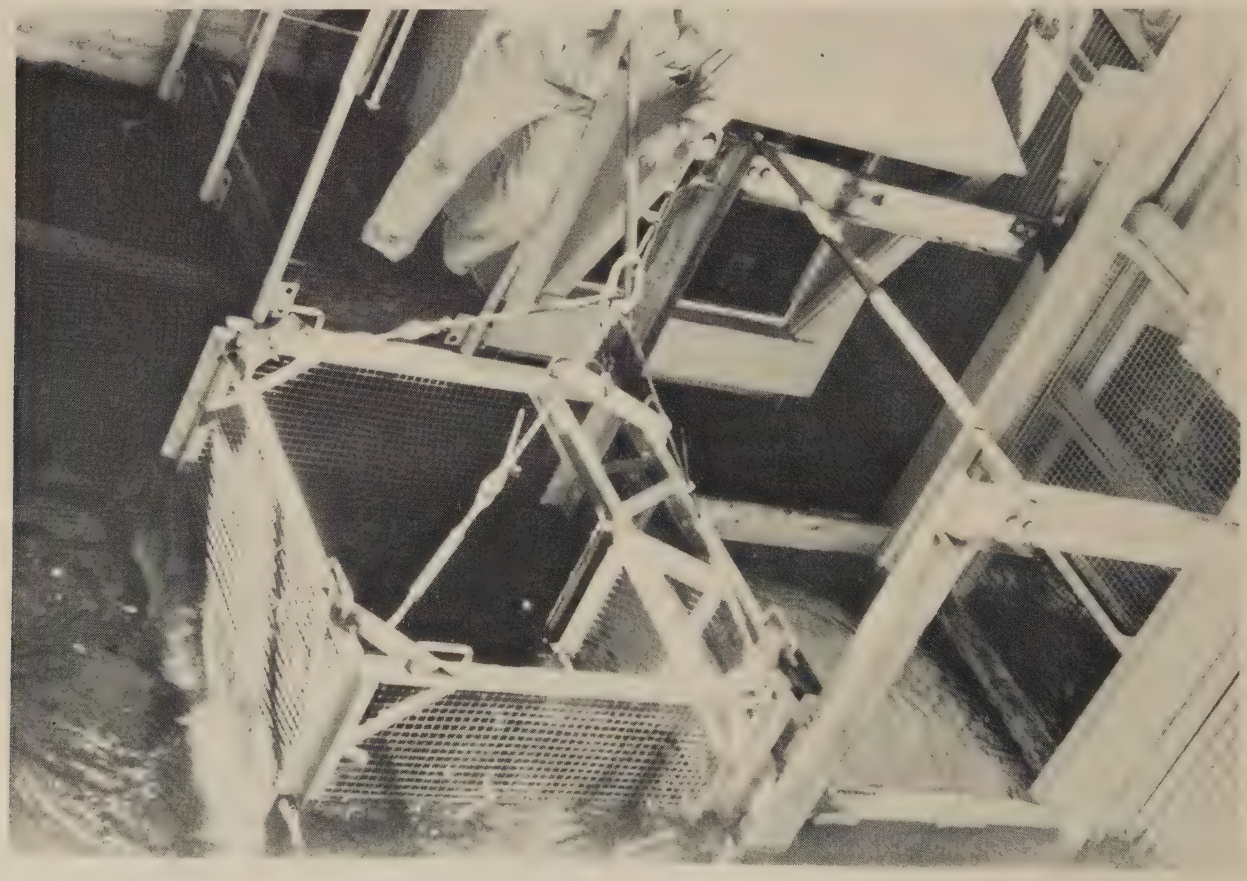

FIGURE 2.—Fishway trap, Rock Island Dam.

amount required to maintain the desired pond level, the surplus water flows either over the top of the dam or is released under lifting gates. Increased flow raises the water depth just below the dam and thereby decreases the velocity of water flowing under the gates. Under these conditions, we saw sockeye salmon swim upstream under the gates, especially when the water depth on the wooden apron just below the dam exceeded 12–18 inches. Consequently, the number of fish passing through the fishways was not always a reliable index of the number passing upstream.

Sockeye salmon have been counted and tags observed (when present) at Rock Island Dam since 1933 and at Rocky Reach Dam since 1961. Complete counts are obtained at Rock Island Dam. During midsummer, when sockeye salmon are migrating, the counting gates near the exits of the three fish ladders are open during daylight but closed at night. At Rocky Reach Dam, on the other hand, the counting gate near the exit of the single fish ladder is open 24 hours daily. Fish are counted 50 minutes per hour from 5 a.m. to 9 p.m. The 50-minute counts are multiplied by 1.2 to estimate the total hourly count. A nighttime correction factor is obtained by counting 24 hours per day once a week. All fish-count data from Rocky Reach Dam used in this report have been corrected by both the hourly and nighttime factors.

STREAM FLOW AND TEMPERATURE

The sockeye salmon migration between Rock Island and Zosel Dams is marked by movement from a larger, cooler river to a smaller, warmer stream. Comparative data on stream flow and temperature are, therefore, potentially important to this study. Data provided by the annual surface-water reports of the U.S. Geological Survey show, however, that the flow of both the Columbia and Okanogan Rivers generally decreases during July and August and has no apparent effect on the migration of sockeye salmon from Rock Island Dam to Zosel Dam.

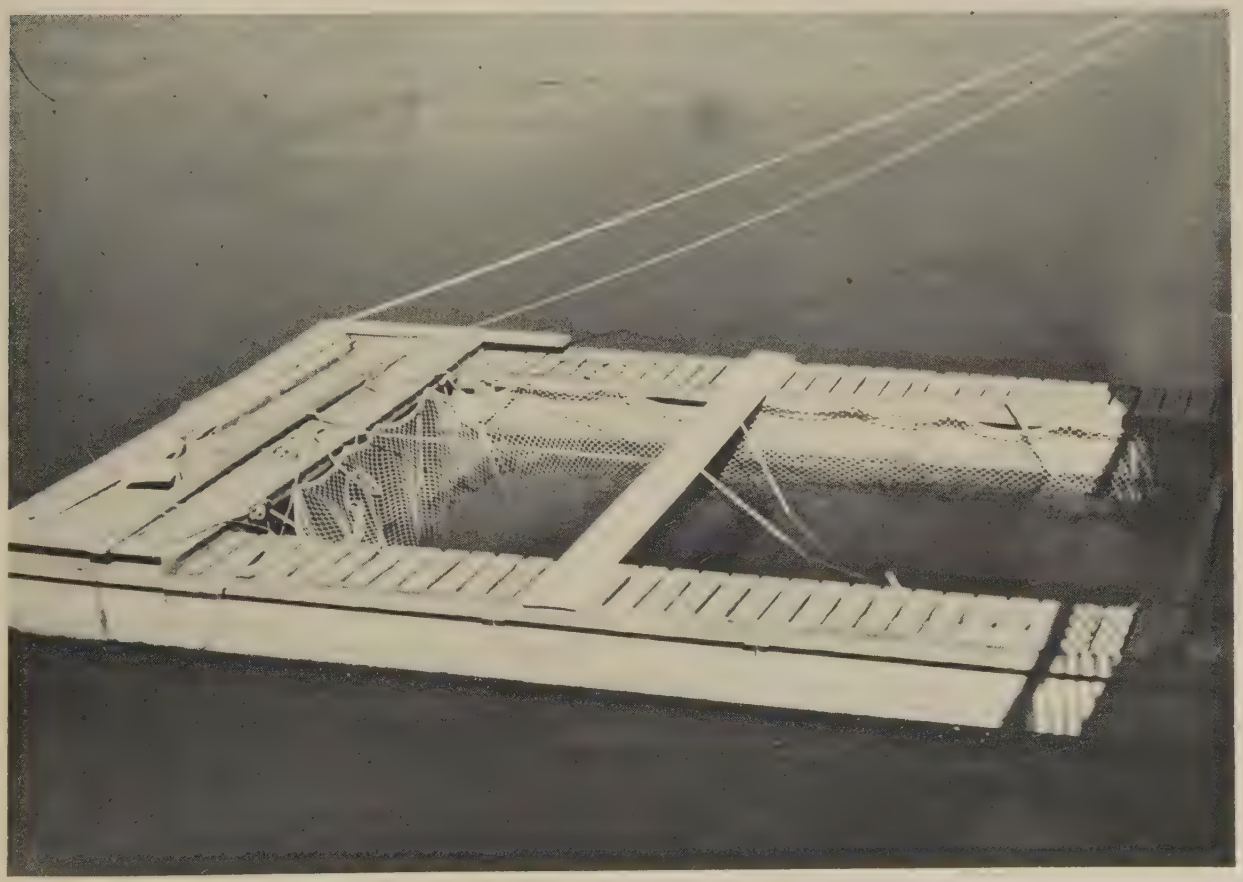

FIGURE 3.—Forebay trap, Rock Island Dam.

Consequently, stream flow is not considered further in our analysis.

It was immediately apparent, on the other hand, from our first observations in 1962 that the water temperature of the Okanogan River greatly influences the migration of sockeye salmon bound for Lake Osoyoos. To understand the effects of temperature better, we have assembled migration-route water temperatures dating back to 1937. Temperature was originally recorded by thermographs or by hand-held thermometers. Daily averages have been computed from the highs and lows on the thermograph charts or from the 8 a.m. and 4 p.m. thermometer readings.

LIMITATIONS AND ADJUSTMENTS OF THE DATA

Before proceeding, it is appropriate to review certain limitations and adjustments of the data that are potential sources of error.

Reliability of the Fish Counts and Tag Observations at Zosel Dam

After 1948, varying proportions of the Okanogan run passed Zosel Dam by means other than the fishways, and the reliability of the counts and tag observations recorded at Zosel Dam since 1948 varies accordingly. We used two criteria to determine which data were adequate for this study. First, by comparing the counts at Zosel Dam with estimates of numbers of fish on the spawning grounds, we calculated the percentage trapping efficiency for 1952–57 and 1962—years for which both fish counts and spawning ground estimates were available. These percentages, however crude, are our best estimates of trapping efficiency at Zosel Dam. Second, we determined from the detailed notes maintained by the fish counters at Zosel Dam whether the modal counts corresponded to the modal numbers estimated to be passing the dam.

Estimates of trapping efficiency are shown in table 2. The overall accuracy of the fish counts in 1955–57 was severely limited. Equally important, the modal counts for those years did not correspond to the modal numbers estimated to be passing the dam. We have accordingly deleted the 1955–57 data from our analysis. Although trapping efficiency was not much higher in 1952, 1954, and 1962, the modal counts agreed closely with the numbers estimated by the counters to be available below the dam. The data for 1952, 1954, and 1962 have been retained, therefore, and, together with the data of high-efficiency years, 1937, 1944, 1953, and 1963, constitute the basis of our evaluation of the effect of water temperature on the migration of sockeye between Rock Island and Zosel Dams. Although no spawning ground estimate was made in 1963, our regular observations indicated a relatively high trapping efficiency at Zosel Dam for that year. A fish-tight weir enabled the counters to make complete fish counts in 1935–37 and 1944. Although the counts of fish were complete in 1935 and 1936, we cannot use them here because there are no water temperature records for those years.

TABLE 2.—*Information on the efficiency of the trapping system at Zosel Dam*

Year	Count of sockeye at Zosel Dam	Spawning-ground estimate[1]	Trapping efficiency
	Number	*Number*	*Percent*
1952	3,217	25,000	13
1953	67,542	34,260	High
1954	3,760	13,206	28
1955	4,130	47,930	9
1956	668	39,256	2
1957	2,019	25,350	8
1962	944	6,405	15

[1] Tufts, Dennis F., and Donovan R. Craddock. 1963. Spawning escapement of Columbia River sockeye salmon (*O. nerka*), 1962. U.S. Bur. of Comm. Fish. Biol. Lab., Seattle, Wash., 17 pp., Jan. 1963 (Processed).

Adjustment of the Tagging Data

French and Wahle (1960) estimated that, before the construction of Rocky Reach Dam, 10.7 days were required for sockeye salmon to migrate from the forebay of Rock Island Dam to Zosel Dam. Their estimate was based on a small sample of 30 tagged sockeye salmon that had been released just above Rock Island Dam in 1954 and 1955 and later observed at Zosel Dam.

To estimate migration time, we have used the large numbers of tagged sockeye salmon (334 and 215) that were released just *below* Rock Island Dam in 1953 and 1954, and later observed at Zosel Dam. Tagged sockeye salmon were released above Rock Island Dam in 1962 and 1963. An adjustment was obviously necessary before the travel time to Zosel Dam of tagged fish that had been released below Rock Island Dam could be compared with the travel time of tagged fish that had been released above Rock Island Dam. We adjusted the data according to the day or days when the number of tagged fish which had been released below Rock Island Dam peaked at the counting stations of Rock Island Dam. The dates of these peaks were treated as dates of release in the forebay. For example, sockeye that

had been released below Rock Island Dam on August 2, 1953, peaked at the Rock Island counting stations on August 4, 1953. In our analysis, therefore, we treated this tagged lot as though it had been released in the Rock Island forebay on August 4. This adjustment made it possible to treat all tagged lots in all years as if they had been released in a common location—the forebay of Rock Island Dam.

Water Temperatures Along the Migration Route

Records of temperatures are frequently lacking from the Okanogan River at Monse and the Columbia River at Brewster, near their confluence, but are available instead from Oroville on the Okanogan River and from Rock Island Dam and Bridgeport on the Columbia River (fig. 4). Certain features are clearly evident in figure 4. First, in July and

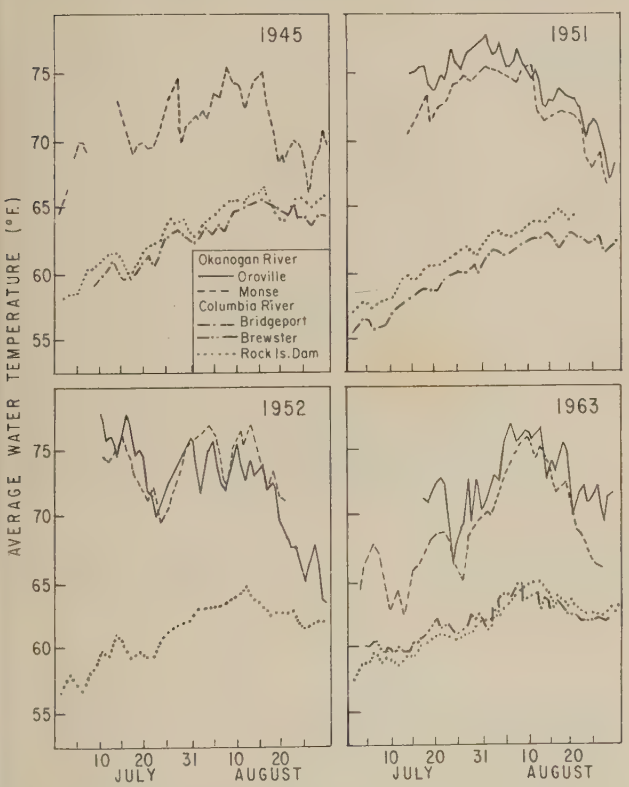

FIGURE 4.—Comparison of Columbia and Okanogan River temperatures, 1945, 1951, 1952, and 1963.

August the Okanogan River is considerably warmer than the Columbia River. Second, in terms of trends (rises and falls over a period of several days) the readings at Oroville and Rock Island (or Bridgeport) reflect the situation in the two streams near their confluence. The absolute readings vary considerably within a river, however, particularly in the Okanogan River, where daily differences occasionally reach 4 or 5° F. (neither station was regularly the higher). Caution must be used, therefore, in comparing the absolute readings from the Oroville and Monse stations.

The methods we describe are not rigorous, and our data are not precise. Yet we believe them to be adequate for the purposes of this report.

TRAVEL TIME BETWEEN DAMS

Travel time of sockeye salmon from Rock Island Dam to Zosel Dam was estimated in 1953 and 1954 before Rocky Reach Dam was built and in 1962 and 1963 after construction. Travel time from Rock Island Dam to Rocky Reach Dam was measured in 1962 and 1963, after Rocky Reach Dam was built.

TRAVEL TIME BETWEEN ROCK ISLAND AND ZOSEL DAMS

In the examination of the basic tagging data for this phase of the study (tables 3–4 and figs. 5–6),

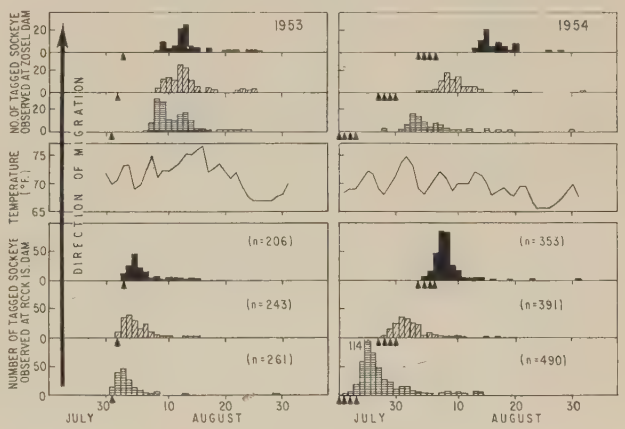

FIGURE 5.—Number of tagged sockeye observed at Rock Island and Zosel Dams after release below Rock Island Dam in 1953 and 1954. The dates of release are designated by triangles below the base lines and the number of fish released is given in parentheses. Daily average temperature of the Okanogan River is given in the center panel.

attention should be given first to the years before Rocky Reach Dam was constructed. In 1953 the sockeye salmon that had been tagged below Rock Island Dam on July 31, August 1, and August 2, peaked at Rock Island Dam on August 2, 3, and 4 in that order, and at Zosel Dam 6, 9, and 9 days later. The tagged fish that were released below

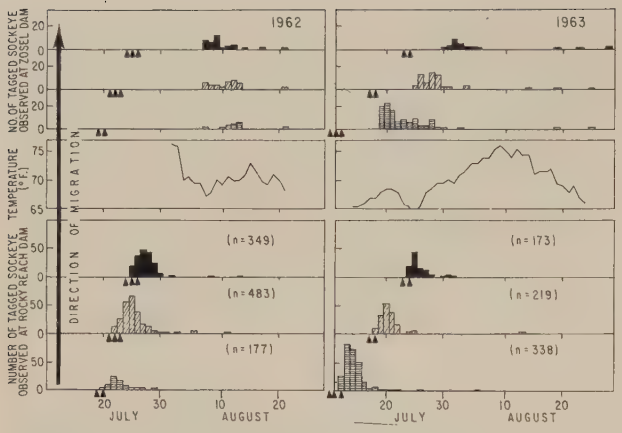

FIGURE 6.—Number of tagged sockeye observed at Rocky Reach and Zosel Dams after release in the Rock Island forebay in 1962 and 1963. The dates of release are designated by triangles below the base lines and the number of fish released is given in parentheses. Daily average temperature of the Okanogan River is given in the center panel.

Rock Island Dam in 1954 have been grouped because of the small numbers which were observed at Zosel Dam. These grouped releases peaked at Rock Island Dam on July 25, July 31, and August 7 and at Zosel Dam 8 to 9, 7 to 8, and 7 to 8 days later.

After Rocky Reach Dam was built, certain changes appeared in the travel time. Tagged sockeye salmon that had been released in the Rock Island forebay on July 19–20, 21–23, and 24–26, 1962, appeared in greatest numbers at Zosel Dam on August 11–13, 7–13, and 7–12. Travel times for the three groups were 22 to 25, 15 to 23, and 12 to 16 days, respectively. The travel times in 1963, on the other hand, were similar to those before Rocky Reach Dam was built—the releases of July 10–12, 17–18, and 23–24 appeared in greatest numbers at Zosel Dam after 7 to 11, 8 to 12, and 8 to 9 days, respectively.

TABLE 3.—*Number of tagged sockeye salmon observed at Rock Island and Zosel Dams after release below Rock Island Dam, 1953 and 1954*

Date of tagging	Number tagged	Point of observations	Date of observation																			
			July											August								
			21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10
1953																							
July 31	261	Rock Island											12	39	45	27	13	9	4	2	5		
		Zosel Dam																	1	8	28	26	11
Aug. 1	243	Rock Island												9	36	40	30	18	24	9	5	4	3
		Zosel Dam																			4	11	12
Aug. 2	206	Rock Island													12	24	46	22	16	3	5	2	4
		Zosel Dam																			1	8	3
1954																							
July 20–23	490	Rock Island	2	6	19	57	114	73	47	26	22	10	11	11	5	3	1	1		2	3	1	3
		Zosel Dam								2			2	6	16	14	9	4	7	6	3	1	1
July 27–30	391	Rock Island								2	16	25	35	34	25	23	3	8	5	2	2	1	1
		Zosel Dam														1	1	1	2	9	17	10	13
Aug. 3–6	353	Rock Island															7	19	48	96	84	26	18
		Zosel Dam																					

TABLE 3.—*Number of tagged sockeye salmon observed at Rock Island and Zosel Dams after release below Rock Island Dam, 1953 and 1954—Continued*

Date of tagging	Number Tagged	Point of observation	Date of observation																			
			August																			
			11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1953																							
July 31	261	Rock Island			1																1		
		Zosel Dam	10	16	17	10	3	3	2		1	1	1	1	2	2							
Aug. 1	243	Rock Island			1	1	1																
		Zosel Dam	10	24	21	10	4		4	1				1	3	1	2						
Aug. 2	206	Rock Island	3	2	1	2	1																
		Zosel Dam	5	21	24	5	4	1	3			1	1	1		2	2	1					
1954																							
July 20–23	490	Rock Island	1		4	2		1															
		Zosel Dam		2			3		1		1											1	
July 27–30	391	Rock Island	1				1		1														
		Zosel Dam	5	5	5	2						1											1
Aug. 3–6	353	Rock Island	4	4	4	4		1			1				1								1
		Zosel Dam			3	10	20	5	8	5	2	7						1		2			

The travel times between Rock Island and Zosel Dams are summarized in table 5. In view of the discrepant results of 1962 and the confinement of the 1953 tagging to the end of the run, the effect of Rocky Reach Dam on the travel time between Rock Island and Zosel Dams is best obtained from the records for 1954 and 1963. The travel times tended to be slightly longer in 1963 than in 1954, but the significance of this small difference is questionable.

In any event, the difference between travel times in 1963 and 1954 is greatly overshadowed by the difference between 1962 and 1963, after Rocky Reach Dam was completed. The travel time in 1962 was much the longer and varied erratically within the season—decreasing as the season progressed. This variability was not evident at Rocky Reach Dam, where the appearance of the various tagged lots was orderly in both years (fig. 6). It is appropriate, however, to examine in greater detail

TABLE 5.—*Travel time of tagged sockeye salmon from Rock Island Dam to Zosel Dam, 1953, 1954, 1962, and 1963*

Year	Date of tagging[1]	Best estimate of travel time
Pre-Rocky Reach:		*Days*
1953	Aug. 2	6
	Aug. 3	9
	Aug. 4	9
1954	July 25	8–9
	July 31	7–8
	Aug. 7	7–8
Post-Rocky Reach:		
1962	July 19–20	22–25
	July 21–23	15–23
	July 24–26	12–16
1963	July 10–12	7–11
	July 17–18	8–12
	July 23–24	8–9

[1] For 1953 and 1954, the dates are those when tagged fish which had been released below Rock Island Dam reappeared in peak numbers at the counting stations of Rock Island Dam.

TABLE 4.—*Number of tagged sockeye salmon observed at Rocky Reach and Zosel Dams after release in the Rock Island Dam forebay, 1962 and 1963*

Date of tagging	Number tagged	Point of observation	Date of observation: July 11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1962																							
July 19–20	177	Rocky Reach										4	10	24	16	8	5	5	1		1		
		Zosel Dam																					
July 21–23	483	Rocky Reach												12	26	55	66	39	18	13	2	1	1
		Zosel Dam																					
July 24–26	349	Rocky Reach															20	38	48	43	22	6	
		Zosel Dam																					
1963																							
July 10–12	338	Rocky Reach	18	24	82	73	50	17	2	6	1	1	1	1				1					
		Zosel Dam									20	23	16	7	8	6	9	3	3	8	1	1	
July 17–18	219	Rocky Reach								10	34	53	39	7		1	2						
		Zosel Dam															3	13	5	15	12	1	1
July 23–24	173	Rocky Reach														20	43	13	12	5		2	4
		Zosel Dam																				2	3

TABLE 4.—*Number of tagged sockeye salmon observed at Rocky Reach and Zosel Dams after release in the Rock Island Dam forebay, 1962 and 1963—Continued*

Date of tagging	Number tagged	Point of observation	Date of observation: August 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1962																														
July 19–20	177	Rocky Reach							1			1	3	4	5								2							
		Zosel Dam																												
July 21–23	483	Rocky Reach		1			5						1																	
		Zosel Dam							6	3	3	2	6	7	5								1							
July 24–26	349	Rocky Reach	1							2					1															
		Zosel Dam							8	6	3	1	3	4		2			2				1							
1963																														
July 10–12	338	Rocky Reach					1																							
		Zosel Dam		1																	1						1			
July 17–18	219	Rocky Reach													1															
		Zosel Dam			4											1					1					1				
July 23–24	173	Rocky Reach	2																											
		Zosel Dam	9	5	2	2	1														1				1					2

the movement of tagged fish between Rock Island Dam forebay and Rocky Reach Dam in 1962 and 1963.

TRAVEL TIME BETWEEN ROCK ISLAND AND ROCKY REACH DAMS

Fifteen lots of tagged fish were released in the forebay of Rock Island Dam in the combined tagging seasons of 1962 and 1963. The reappearance of these lots at Rocky Reach Dam 15 miles upstream varied little; 12 peaked on the second day, 1 on the first day, and 2 on the third day after release.

We plotted the observations of tags at Rocky Reach Dam by 4-hour intervals (fig. 7). Only the

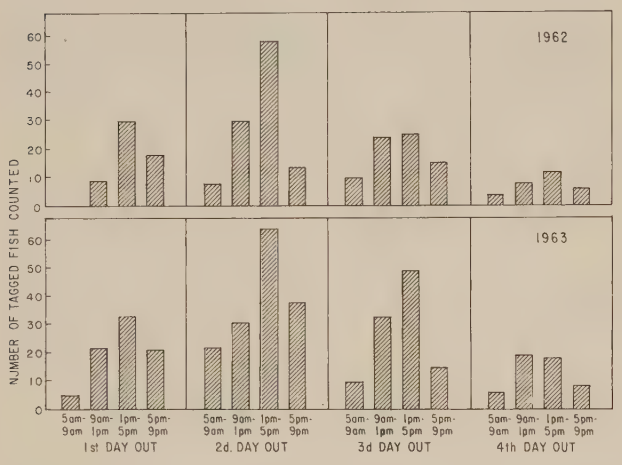

FIGURE 7.—Number of tagged sockeye counted over Rocky Reach Dam in different 4-hour periods during the 4 days after release in the Rock Island forebay in 1962 and 1963. The periods (shown at the bottom of the graph) were 5 a.m.–9 a.m., 9 a.m.–1 p.m., 1 p.m.–5 p.m., and 5 p.m.–9 p.m. Counting was discontinued between 9 p.m. and 5.a.m.

tags observed during the first 4 days after release have been included because tagged fish became scarce after the fourth day. Fish tagged on July 17 and 19–21, 1962, have not been included because the precise time that these fish passed Rocky Reach Dam was not recorded. The agreement of the data for the 2 years is extremely close. For each release the greatest numbers of tags were observed at 1 p.m. to 5 p.m. on the second day after release. If we consider 10 a.m. as the average release time and 3 p.m. (the midpoint of the 1 p.m. to 5 p.m. period) on the second day out as the average time when tagged fish passed Rocky Reach Dam, the modal travel time was 53 hours. Diurnal consistency is also evident: seven times in eight the numbers of tags observed increased from the first 4-hour period (5 a.m. to 9 a.m.) to the second (9 a.m. to 1 p.m.), peaked during the third period (1 p.m. to 5 p.m.), and decreased during the last (5 p.m. to 9 p.m.).

The consistency of the data indicates that fish passage was uniform and orderly at Rocky Reach Dam in 1962 and 1963, and that the much greater travel time from Rock Island Dam to Zosel Dam in 1962 must be attributed to longer travel time above Rocky Reach. Thus, it is necessary to look to the stretch between Rocky Reach Dam and Zosel Dam for the causes of the slow travel time.

EFFECTS OF WATER TEMPERATURE ON THE MIGRATION OF SOCKEYE SALMON

On August 1, 1962, after sockeye had failed to appear at Zosel Dam despite high counts at Rocky Reach Dam, the 133-mile migration route between Rocky Reach and Zosel Dams was searched by plane for schools of salmon. Despite optimum aerial-survey conditions, not a single sockeye salmon was sighted—evidence that the run had not yet entered the Okanogan River.

On August 2, the following day, I (Major) visited the area on the bank of the Columbia River immediately adjacent to the confluence of the Okanogan and Columbia Rivers—a traditional fishing site of the Colville Indians. Of the 8 to 10 Indians present, only 1 responded to questions. He answered that "blueback (sockeye) were milling in the area and fishing was getting better every day."

Sockeye salmon did not reach Zosel Dam until August 7; at that time the counter reported several hundred below the dam and captured 155 in the traps, including 15 with tags. Tag recoveries included individuals from six of the seven lots. This breakdown of the usual chronological order, and the resultant mixing and accumulation of the various segments of the run, indicated that the run had been delayed. Information from the aerial search and from the Indian's report pinpoints the delay at the confluence of the Okanogan and Columbia Rivers.

We hypothesized that the sockeye salmon had been blocked from the Okanogan River by unfavorably high water temperatures until a sharp temperature drop on August 2–3 permitted them to enter the stream on or about August 3 and to reach Zosel Dam on August 7.

To examine the validity of the general hypothesis

as it applies to all years, we shall use fish counts and water temperatures along the migration route for 1937, 1944, 1952–54, 1962, and 1963 (table 6 and figs. 8–10). For years when sockeye salmon were tagged (1953, 1954, 1962, and 1963), we will re-examine as part of the analysis the tagging data in figures 5 and 6.

Although the data, particularly the fish counts at Zosel Dam, are not precise enough for us to make

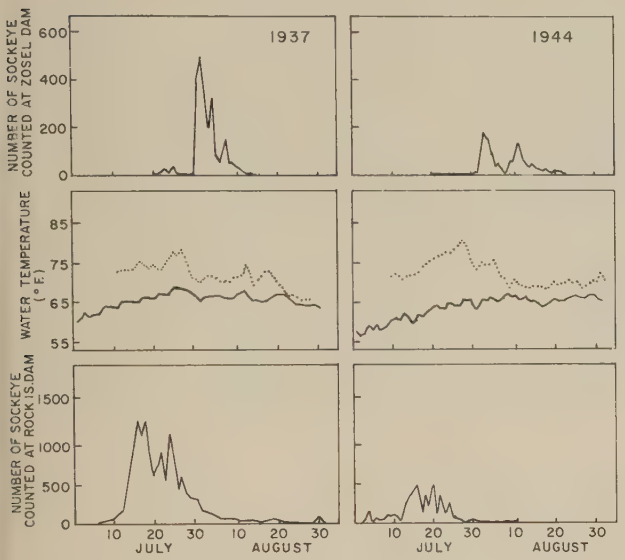

FIGURE 8.—Number of sockeye salmon counted at Rock Island and Zosel Dams, July and August, 1937 and 1944. Average temperatures of the Okanogan (dotted line) and Columbia (solid line) Rivers are given in the middle panel.

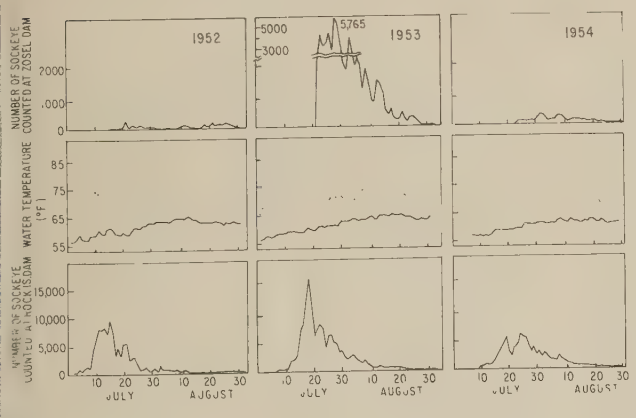

FIGURE 9.—Number of sockeye salmon counted at Rock Island and Zosel Dams, July and August, 1952, 1953, and 1954. Average temperatures of the Okanogan (dotted line) and Columbia (solid line) Rivers are given in the middle panel.

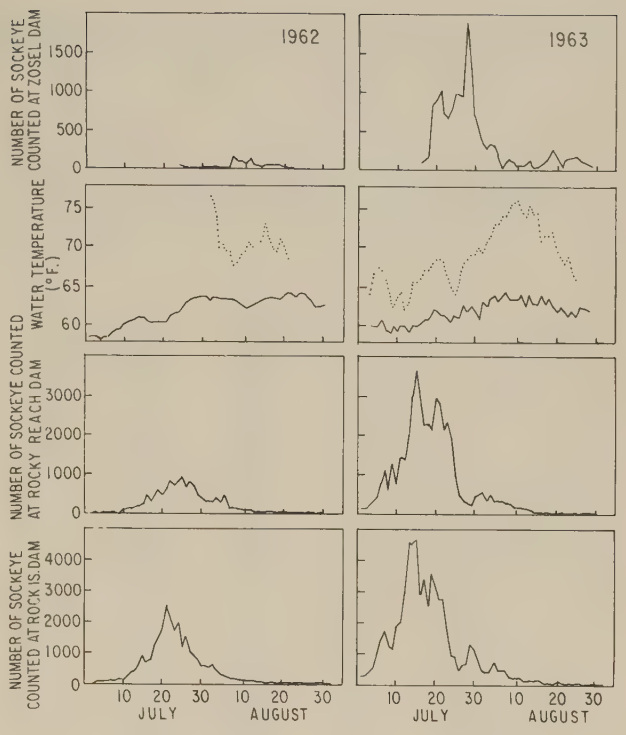

FIGURE 10.—Numbers of sockeye salmon counted at Rock Island, Rocky Reach, and Zosel Dams in 1962 and 1963. Average temperatures of the Okanogan (dotted line) and Columbia (solid line) Rivers are given in the second panel from the top.

a quantitative analysis of the relations involved, we do have evidence pertinent to our hypothesis that unfavorable water temperature (or related factors) blocks the sockeye salmon from the Okanogan River until falling temperatures allow the migration to continue.

Figures 8 to 10 establish clearly the general relation between temperature and movement of fish in the Okanogan River. When fish are presumably available to the river, highs and lows in the count at Zosel Dam not evident in the counts at Rock Island Dam or Rocky Reach Dam, regularly follow falling and rising temperature in the Okanogan River. This relation is particularly striking when the temperature drop is preceded by prolonged high temperatures. No influence of the temperature of the Columbia River on the upstream migration of sockeye salmon is apparent.

Knowledge of the normal travel time from Rock Island Dam to Zosel Dam under favorable temperature conditions is highly relevant to an understanding of the effects of unfavorable temperatures

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Dams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963*

Date	1937				1944				1952				1953			
	Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.
July 1	0			60.0	3			57.5	68			56.5			66.5	56.0
2	0			60.5	4			56.5	132			56.5			68.0	56.5
3	0				8			57.0	329			57.5			70.0	57.5
4	1			62.5	148			58.5	998			58.5			69.0	57.5
5	1			61.5	56			58.0	739			57.5			70.0	57.0
6	1			62.0	72			59.0	1,019			57.0	5		71.5	57.5
7	1			62.0	60			58.0	1,232			57.0	31		73.5	58.0
8	2			62.5	85			58.5	1,143			58.5	96		73.5	58.5
9	1			64.0	128			59.5	4,777			58.5	146		74.5	58.5
10	0			64.0	126		71.5	60.5	6,810		74.5	59.5	232		74.5	58.5
11	8		72.5	64.0	110		72.0	61.0	8,135		74.0	60.5	375		74.5	59.0
12	13			64.0	58		71.5	60.5	7,981		74.5	59.5	1,626		74.5	59.0
13	156		73.0	64.5	255		70.5	62.0	8,293		75.5	59.5	2,094		73.0	59.5
14	425		73.0	65.5	355		71.5	61.0	7,200		76.0	61.0	2,732		72.5	59.5
15	962		73.0	65.5	402	0	71.5	59.5	9,581	0	76.0	61.5	7,332		73.0	58.5
16	1,317		74.5	65.5	455		72.0	60.5	7,728	0	74.5	60.5	8,201		74.5	58.5
17	1,171		75.0	65.5	170		72.5	62.0	3,797	0	74.0	59.5	11,984		76.0	59.5
18	1,288		74.5	66.0	378		73.5	61.5	4,790	0	73.0	59.5	15,355		76.0	60.5
19	925		73.5	66.5	237			62.5	3,544	0	72.5	59.5	11,348		73.5	60.0
20	670	1	74.0	66.5	460		72.5	63.5	5,435	7	72.5	60.0	6,240		73.5	59.5
21	738	1	73.5	66.5	136		75.5	64.0	5,490	287	71.0	59.5	7,403	10	74.5	59.5
22	929	10	73.5	66.5	398		76.5	63.5	2,644	70	72.5	59.5	8,158	2,090	73.0	60.5
23	595	15	74.0	67.5	137		77.0	63.0	2,850	107	69.5	60.5	7,464	4,175	72.0	61.0
24	1,125	3	76.0	67.5	249		78.0	64.5	2,851	125	69.5	61.5	4,166	3,293	71.0	60.5
25	756	23	77.5	67.5	83		78.0	64.5	2,037	63	70.5	61.5	6,327	3,576	70.0	61.0
26	479	8	77.0	68.5	47		78.0	64.0	847	99	72.0	61.5	6,397	4,463	70.5	61.0
27	622	3	78.0	68.5	66		79.5	64.0	882	90	72.5	62.0	5,191	3,059	71.0	61.5
28	461	3	75.5	68.5	59		80.5	65.0	904	74	73.5	62.0	4,929	5,765	71.0	61.5
29	366	3	74.0	68.0	34		79.0	65.5	490	52	75.5	62.5	3,419	5,180	72.5	61.5
30	268	0	71.0	68.0	38			65.5	403	34		62.5	3,692	3,396	71.5	62.5
31	299	393		67.0	17		74.0	63.0	914	10		62.5	2,953	2,153	70.0	62.5

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Dams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963—Continued*

Date	1937				1944				1952				1953			
	Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature		Sockeye		Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.	Number	Number	°F.	°F.
Aug. 1	198	494	70.5	66.5	9	0	73.0	63.5	492	11	76.5	63.5	2,161	1,891	70.5	62.5
2	62	343	71.0	65.5	28	4	75.0	65.5	1,324	3	76.0	63.5	2,499	2,823	73.0	62.5
3	80	200	71.5	66.0	12	176	74.0	65.5	907	1	77.0	63.5	2,875	3,959	73.0	63.5
4	100	336	71.5	66.5	14	157	74.5	66.0	874	0	77.0	63.5	2,433	1,984	69.0	63.5
5	101	81	70.5	66.5	11	95	75.5	65.5	726	2	76.0	63.5	1,809	2,310	69.5	63.0
6	79	60	70.0	66.5	6	20		66.5	743	4	74.0	63.5	1,651	2,076	72.5	63.5
7	6	139	70.0	66.5	16	39	71.5	66.5	686	1	73.5	64.0	1,899	1,314	74.5	63.5
8	0	59	70.0	66.0	20	17	71.0		788	0	74.0	64.0	1,462	1,864	71.0	63.5
9	190	35	71.0	66.0	4	2	69.0	66.0	587	13	76.0	64.5	1,177	1,676	72.0	64.0
10	48	14	71.5	66.0	0	54	70.5	65.0	392	68	76.5	64.5	746	950	72.0	64.5
11	47	4	71.5	66.5	1	55	70.0	65.5	250	136	75.5	64.5	444	882	73.0	63.5
12	21	13	74.0	67.5	2	117		65.0	408	55	76.5	65.5	436	1,676	73.5	63.5
13	44	8	72.5	68.0	5	57	70.0	65.0	218	21	77.5	65.0	807	1,551	75.0	64.5
14	53		69.0	66.0	5	19	70.0	64.5	187	2	75.0	64.0	758	1,152	75.0	64.5
15	22		70.5	65.5	3	31	70.0	64.0	183	1	74.5	64.0	487	698	76.0	64.5
16	44		71.5	65.5	7	12	69.5	64.5	116	0	73.0	63.5	361	376	76.5	64.5
17	32		72.5	65.5	4	11	69.5	65.0	101	0	73.5	63.0	333	610	72.0	65.0
18	38		72.5	65.5	3	13	70.0	65.5	138	148	71.5	63.0	287	311	72.5	65.0
19	70		71.5	66.0	1	4	69.0	65.0	114	124	71.5	63.0	226	209	73.5	64.5
20	32		70.5		2	1	69.5	65.0	123	104	71.5	63.0	172	214	72.0	64.5
21	19			67.5	0	5	70.0	65.5	175	201		63.0	74	525	71.0	64.5
22	11		67.5	67.0	2	2	70.5		79	93		63.5	68	292	72.0	64.0
23	18		66.0	66.0	1	0	69.5		42	115		63.0	146	191	69.0	64.0
24	12		66.5	65.5	1	1	70.0	66.0	76	169		62.5	69	335	67.5	64.0
25	8		66.0	64.5	3	1	68.5	66.0	34	148		62.0	47	346	67.0	63.5
26	0		65.3	64.5	0	2	69.0	66.0	46	186		62.5	37	65	67.0	62.5
27	6		65.3	64.0	1	1	69.5	66.5	38	164		62.5	29	28	67.0	62.5
28	3		65.3	64.0	0		70.5	66.5	34	119		62.5	22	74	67.0	63.5
29	0			64.0	1		70.0	66.5	12	13		63.0	60		67.5	63.5
30	79			64.0	0		72.5		14	60		62.5	12		68.0	63.5
31	24			63.0	1		70.5	65.5	9	26		62.5	9		70.0	64.5

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Dams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963—Continued*

Date	1954				1962					1963				
	Sockeye		Temperature		Sockeye			Temperature		Sockeye			Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.
July 1	7		64.5		40	0			58.5	285	121			57.5
2	8		64.0		16	0			58.5	287	131			59.0
3	15		66.5		23	4			58.5	484	196		64.0	59.0
4	27		68.5		36	8			58.5	521	299		66.5	59.5
5	39		70.0		54	12			58.0	1,023	406		67.5	59.5
6	93		69.5		69	26			58.5	1,401	732		67.0	59.5
7	136		68.5	56.5	90	28			59.0	1,719	1,123		66.0	59.0
8	182		68.0	57.0	163	22			59.5	1,291	602		64.0	59.5
9	272		69.0	56.5	96	43			60.0	1,238	1,277		62.5	59.0
10	375		65.5	57.0	140	66			60.5	1,819	807		63.5	58.5
11	398		67.0	56.5	292	66			60.5	1,971	1,426		64.0	59.0
12	768		68.0	57.0	389	66			61.5	2,893	1,337		62.0	59.5
13	715		70.0	57.0	416	140			61.0	4,567	2,042		63.0	59.5
14	843		72.0	57.5	638	166			61.0	4,548	2,981		65.5	59.5
15	1,158		73.5	58.5	932	235			61.5	4,601	3,636		65.5	59.5
16	2,383		74.5	58.5	745	415			61.5	2,986	2,891	114	66.0	60.5
17	3,396		74.5	58.5	788	334			61.0	3,300	2,367	148	67.0	60.5
18	4,368		74.0	58.5	1,272	474			60.5	2,653	2,321	187	67.0	60.5
19	5,440		72.5	58.5	1,587	553			60.5	3,572	2,171	810	68.0	61.0
20	3,417		68.0	58.5	1,733	454			61.0	3,116	2,888	898	68.5	61.0
21	2,136		68.5	58.5	2,541	571			61.0	2,734	2,783	1,018	68.5	61.5
22	3,778		69.0	58.5	2,133	800			61.5	2,725	2,127	766	68.0	61.5
23	4,178	9	69.0	59.5	1,702	708			62.5	1,814	2,308	626	66.0	61.5
24	5,908	117	70.5	59.5	1,956	803	51		62.5	886	1,901	776	65.5	60.5
25	5,811	101	72.0	59.5	1,237	856	32		62.5	841	932	971	64.0	60.5
26	5,584	110	71.5	60.5	1,544	683	1		63.0	475	438	968	65.5	60.5
27	4,137	87	69.0	60.5	1,160	793	1		63.5	633	315	934	68.0	60.5
28	3,347	74	68.0	60.5	880	670	8		64.0	1,015	307	1,900	68.5	61.0
29	3,753	61	69.5	60.5	853	480	0		64.0	1,267	215	1,233	69.5	62.0
30	2,815	117	71.0	60.5	573	460	0		63.0	1,138	479	768	69.5	62.0
31	2,913	226	73.5	61.0	666	315	0		62.5	753	546	482	70.0	62.0

TABLE 6.—*Counts of sockeye salmon passing Rock Island, Zosel, and Rocky Reach Rams, and Okanogan and Columbia River temperatures, 1937, 1944, 1952-54, 1962, and 1963—Continued*

Date	1954				1962					1963				
	Sockeye		Temperature		Sockeye			Temperature		Sockeye			Temperature	
	Rock Is. Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River	Rock Is. Dam	Rocky Reach Dam	Zosel Dam	Okan. River	Col. River
	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.	Number	Number	Number	°F.	°F.
Aug. 1	2,158	386	74.5	61.5	503	344	0	76.5	62.5	490	594	356	69.5	62.0
2	2,573	311	73.0	61.5	583	365	0	76.0	61.5	380	198	281	71.0	62.0
3	1,654	159	69.0	61.5	489	298	0	70.0	62.0	491	484	305	71.5	62.5
4	1,506	88	68.0	61.0	360	232	2	70.5	62.5	706	327	248	73.0	63.0
5	1,542	130	69.5	61.0	273	400	2	69.5	61.5	513	309	83	73.0	63.5
6	1,415	146	71.0	61.5	196	139	16	69.5	62.0	469	339	20	74.0	64.0
7	1,832	234	72.0	61.5	174	142	155	67.5	62.0	360	241	101	74.0	64.0
8	1,575	280	71.0	62.0	168	112	102	68.0	62.5	222	219	149	75.5	64.5
9	1,317	234	68.5	62.5	94	109	100	70.0	61.5	242	183	31	76.0	64.5
10	975	126	70.0	62.0	76	73	61	69.5	61.0	197	172	29	75.0	64.5
11	913	106	70.0	61.5	116	61	135	70.5	60.5	152	128	38	74.0	
12	752	103	70.0	61.5	116	73	96	70.0	60.5	132	78	0	75.5	
13	527	116	72.0	62.5	100	81	46	70.0	61.5	154	68	43	74.5	64.5
14	718	118	71.5	62.0	67	61	11	71.0	61.5	192	51	116	74.5	63.5
15	502	104	70.0	61.5	65	50	31	73.0	62.0	189	42	42	71.0	63.5
16	332	47	68.0	61.5	101	46	17	71.5	62.0	58	55	47	71.5	64.0
17	320	57	68.5	61.5	59	45	15	70.0	62.5	74	37	12	71.5	63.5
18	349	45	69.0	62.0	65	54	3	69.5	62.0	70	10	159	72.0	63.0
19	279	42	68.0	62.0	52	18	14	71.0	62.0	67	9	257	69.5	63.5
20	177	46	68.0	62.5	63	18	6	70.0	62.5	51	12	107	69.0	62.5
21	129		69.5	62.5	43	17	24	68.5	62.5	71	16	36	68.0	62.5
22	173		69.5	62.0	61	22	15		62.5	48	8	117	69.0	62.5
23	105		66.5	61.5	38	15			62.5	55	4	141	67.0	62.5
24	144	3	65.5	62.0	30	42			62.5	33	4	166	66.0	62.5
25	67	12	65.5	61.5	38	14			62.5	38	29	170		62.5
26	78	26	65.5	60.5	29	8			62.5	53	5	125		62.0
27	54	10	66.0	61.0	54	8			61.5	28	26	108		63.0
28	44	10	67.0	61.0	39	18			61.5	32	52	99		62.5
29	40	9	68.0	61.5	38	9			61.5	28	9	48		62.5
30	39	14	69.5	61.5	36	11			62.0	13	49			63.0
31	33	17	67.5	62.0	17	8			62.5	12	25			63.5

on the migration of sockeye salmon. As has been brought out earlier, the travel time was 8 to 9, 7 to 8, and 7 to 8 days for the three groups tagged in 1954 before Rocky Reach Dam was constructed. In 1963, after Rocky Reach Dam was completed, the most frequent time was 9 days. On the basis of these travel times, we may assume that the sockeye salmon arrive at the mouth of the Okanogan River, 80 miles above Rock Island Dam or roughly halfway on the 154-mile distance from Rock Island Dam to Zosel Dam, on the fourth or fifth day after passing Rock Island Dam. Accordingly, the remaining 3 to 5 days of the typical 8- or 9-day total migration time are spent negotiating the 74-mile route from the confluence to Zosel Dam.

Under this assumption, we can retrace the migration of certain segments of the runs in several years. In 1937, for example, fish were abundant at Rock Island Dam beginning July 13. Had the Okanogan-bound segment of this run moved without delay, we would have expected it at Zosel Dam beginning July 21. Yet, the counts at Zosel Dam remained practically nil until July 31—3 days after the temperature of the Okanogan River began a sharp decline. Prior to July 28, the temperature had been either relatively stable or climbing sharply; either condition apparently delayed the fish—some as long as 10 days.

The events of 1937 were essentially repeated in 1944; fish counts increased significantly at Rock Island beginning July 13, 1944, but not at Zosel Dam until August 3—5 days after the water temperature decreased on July 29 and up to 13 days later than expected. Then, following several days of high counts, the number of sockeye salmon arriving at Zosel Dam dropped sharply, finally reaching a low of two fish on August 9. These low counts corresponded with rising or stable water temperatures. The count surged again on August 10—3 days after a sharp drop in water temperature.

Fish migration was similar in 1952. Counting of fish began at Zosel Dam on July 15, but no sockeye salmon were seen until the evening of July 20, when seven were taken in the traps. The count increased markedly the next day, and sockeye salmon were relatively abundant the following 9 days. This increased abundance of fish began 5 days after the beginning of a temperature drop which eventually lasted 9 days. Then, beginning July 25, the temperature rose steadily until August 5, when it began to decline. This second rise in temperature brought a second period of low counts which lasted until August 10—5 days after the temperature fell on August 5. Movement was suppressed a third time by a general 6-day rise in temperature from August 8 to 13. A decrease of temperature on August 14 resulted in a surge of fish at Zosel Dam on August 18—4 days later. Thereafter, the temperature dropped steadily and, judging by the counts, fish migration through the area was unimpeded.

The counts at Zosel Dam in 1953 generally reflected the counts at Rock Island. This agreement probably occurred because increases in water temperature were short (2–4 days) and were followed by falling temperatures during the time when the greater portion of the run was migrating through the critical area.

A late-season temperature rise on August 6–7, 1953, coincided with the arrival of tagged fish. This event provides the first opportunity to study the effects of water temperature in terms of a marked segment of the population. For this analysis, we need to refer to figure 5, which depicts the Okanogan River temperatures and the movement of tagged fish from Rock Island to Zosel Dam. On the assumption that the normal travel time from Rock Island Dam to the confluence of the two rivers is 4 to 5 days, we reason that some individuals from the lot tagged on July 31 reached the confluence on August 4 or 5, before the temperature rise of August 6–7. These early arrivals peaked initially at Zosel Dam on August 8. The rising water temperatures on August 6–7 suppressed entry of the later arrivals into the Okanogan River until a drop of temperature on August 8. This decrease of temperature resulted in another surge of tagged fish at Zosel Dam on August 11 to 12, and gave the count of tagged fish at Zosel a bimodal distribution not evident at Rock Island. Apparently, few fish from the lot tagged on August 1 arrived at the river mouth before the temperature rose; most arrived during the rise of August 6 to 7 and therefore did not appear at Zosel Dam until August 12—4 days after the temperature fell on August 8. Similarly, few fish from the lot tagged on August 2 arrived at the confluence before the temperature rise suppressed their entry. Most of these fish arrived at Zosel Dam on August 12 to 13—4 or 5 days after the temperature drop.

The movement of the various tagged segments of the 1954 run can also be retraced from figure 5.

Fish released below Rock Island Dam on July 20–23 peaked at Rock Island Dam on July 25, and at Zosel Dam on August 2–3, 8 to 9 days later. From these records we infer that most of the tagged fish reached the Okanogan River on July 29, when the temperature was just beginning to increase, and that this increase did *not* suppress entry to the stream. Similarly, the collective releases of July 27–30 peaked at Rock Island Dam on July 31 to August 1 and at Zosel Dam on August 8. On the assumption of 4 days for travel, we estimate that most of these fish arrived at the mouth of the Okanogan on August 5–6 when the temperature began a new rise. Again, however, migration was not affected. Finally, the August 3–6 releases of tagged fish peaked at Rock Island Dam on August 7–8 and probably arrived at the mouth of the Okanogan River on August 11–12, when temperatures were fairly stable. These fish also appear to have migrated freely through the Okanogan River. A possible explanation of the normal progress of the migration despite rising temperatures is given below in our discussion of the 1963 migrations.

Temperatures of the Okanogan River were not recorded in 1962 until August 1. High air temperatures indicate, however, that the water temperature almost surely had been rising prior to August 1. Rising temperature would account for the July 26 to August 5 lull in the count at Zosel Dam (figs. 6 and 10). On the basis of counts at Rocky Reach Dam, we would have expected the arrival of sockeye salmon, both tagged and untagged, at Zosel Dam during this interval. The arrival of the fish at the mouth of the Okanogan River coincided, however, with rising water temperatures, a condition which apparently blocked their entry.

The 1963 migration progressed from Rocky Reach Dam to Zosel Dam without major delay (figs. 6 and 10). Tag recoveries were orderly in contrast to those of 1962; peaks at Zosel Dam followed comparable peaks at Rocky Reach Dam by 6, 6 to 8, 6, 7 to 9, 6 to 9, and 6 to 10 days. Thus, migration was normal in 1963, despite generally rising water temperatures.

The absence of delay in 1954 and 1963, despite rising water temperatures, focuses attention on the importance of the level at which the temperature is changing. For example, migration was unimpeded by rising temperatures in the 62° to 69° F. range in 1963, but was halted by rises in the 75° to 78°, 70° to 77°, and 74° to 78° F. ranges in 1952.[2] Furthermore, a temperature rise in the 73° to 78° F. range at Oroville interrupted the migration in 1937, a year in which occasional temperature readings taken at Monse on the lower Okanogan River were even higher than those at Oroville (Chapman, 1941). On the other hand, the 1954 migration was apparently unaffected by rises in the 68° to 70° F. range. The dependability of the latter example is subject to some question, however, because the temperature readings were recorded at Oroville, not at Monse.

These several examples suggest a threshold temperature of about 70° F., below which migration is not affected, but above which rising or stable temperatures inhibit migration—a condition which endures until a sharp drop allows the migration to resume.

We have not considered here a situation in which fish enter the Okanogan River under favorable conditions only to be confronted enroute by sharply rising water temperatures. We have no data on this aspect of the problem, but suspect that the behavior and survival of the fish depend on several factors, including: (1) their location at the time they are confronted by rising temperatures; (2) their ability to acclimate; (3) their size, general health, and stage of maturity; and (4) the level to which the water temperature rises.

RESULTS OF OTHER STUDIES AND THEIR POSSIBLE BEARING ON THE PROBLEM IN THE OKANOGAN RIVER

The environmental factors that control the migrations of adult Pacific salmon have long been of practical and theoretical interest to fishery biologists. The literature gives many examples of environmental influences that affect different populations in different ways. Rather than present another review of the extensive literature on this broad subject, a matter so capably handled by Hoar (1953) and Allen (1956), we refer here only to the more important papers that deal with the environmental factors that influence the sudden mass movement of migrating salmon.

Several investigators have found that rainfall and streamflow affect the migration of adult salmon. Pritchard (1936), and Davidson, Vaughan, Hutchinson, and Pritchard (1943), who studied pink

[2] These temperatures, recorded at Monse, are not subject to the possible error of estimating temperatures in the lower river from actual readings at Oroville.

salmon (*O. gorbuscha*), and Hunter (1959), who worked with pink salmon and chum salmon (*O. keta*), concluded that entry into a river follows increases in stream flow. Shapavalov and Taft (1954) noted a correlation between the general periods of the spawning runs of silver salmon (*O. kisutch*) and rainfall. They further believed, but were unable to demonstrate quantitatively, that fish movement increased with a rise of stream flow. Allen (1956), on the other hand, related the movement of silver salmon and chinook salmon (*O. tshawytscha*) to nighttime rainfall and low barometric pressure, respectively. Ellis (1963) believed that the entry of silver salmon and sockeye salmon into rivers was associated with the appearance of atmospheric warm fronts over the estuary.

Only Foerster (1929) and Cramer and Hammack (1952) attributed the sudden movement of salmon to changes in water temperature. Foerster, who reported on sockeye salmon at Cultus Lake, British Columbia, noted that the numbers of fish arriving at a counting fence synchronized closely with temperature change; increases in the daily run accompanied declines in temperature. Cramer and Hammack, who studied chinook salmon in Deer Creek, a tributary to the Sacramento River, Calif., concluded that at the close of a period of clear weather and relatively cool water, sudden increases in water temperature to 75° F. caused an upsurge of fish.

Andrew and Geen (1960), in their appraisal of all available information on the possible effects of dam construction on the Fraser River, British Columbia, devoted considerable attention to the effects of temperature and delay on upstream-migrating salmon. High water temperatures, they concluded, are detrimental to salmon in their upstream migration because they increase the rate of energy consumption and the incidence of disease and parasites, and may be directly lethal.

In the matter of delay, Andrew and Geen (1960) cited Thompson (1945) as having shown that a delay of 12 days at Hell's Gate (before construction of the fishways) was sufficient to prevent sockeye salmon from reaching their spawning grounds, and that lesser delays reduced the reproductive capacity of the fish. The same authors also referred to an incident in the Fraser Canyon at Yale, British Columbia, in 1955 where the early run to the Stuart River was blocked 6 days by high water. Of an estimated 30,000 to 35,000 sockeye salmon, only 2,170 reached the spawning grounds.

The effect of delay on the productivity of salmon has been illustrated by studies of fish passage at a rock slide on the Babine River, British Columbia (Godfrey, Hourston, Stokes, and Withler, 1954). Concerning this study, Andrew and Geen (1960) stated:

> . . . . Tagging of fish below the point of difficult passage and recovery of the tagged fish at a counting fence 40 miles upstream showed that some of the fish delayed below the obstruction were able to migrate to their spawning grounds but relatively few were able to spawn successfully. Because fish were delayed and weakened below the obstruction they were not able to migrate at a normal rate after passing the obstruction. The effective spawning in 1952, when some sockeye were delayed for extended periods, was estimated as 30 to 42 percent of the numbers of female sockeye that reached the spawning grounds or 7 to 10 percent of the total escapement. From 30 to 40 percent of the female sockeye examined on the spawning ground died unspawned and others died after passing the obstruction but before reaching the spawning grounds.

The previous references indicate that salmon that have been delayed enroute to spawning grounds can be affected in two ways. First, some die enroute to the spawning grounds and second, some complete the journey but are unable to spawn successfully. We conclude that temperature blocks of the type outlined in this paper similarly affect sockeye salmon bound for the Okanogan River spawning grounds.

SUMMARY

Sockeye salmon were tagged at Rock Island Dam and later observed at Zosel Dam on the Okanogan River in 1953–54 and 1962–63. These experiments were used to detect any changes in the migration time caused by Rocky Reach Dam, which was constructed on the migration route during the intervening years.

Travel time varied greatly, both between and within years. The difference between 1962 and 1963 exceeded the difference between 1963 and 1953–54. The best estimate of the time required for sockeye salmon to migrate from Rock Island Dam to Zosel Dam is 7 to 9 days. barring major delay due to environment. This travel time has not been increased by Rocky Reach Dam.

Water temperature of the lower Okanogan River, or factors linked with it, is by far the greatest source of delay. Below 70° F., entry into the Okanogan River is relatively unimpeded. Above 70° F., relatively stable or rising temperatures delay entry until a sharp drop occurs.

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SEASONAL OCCURRENCE AND SIZE DISTRIBUTION OF POSTLARVAL BROWN AND WHITE SHRIMP NEAR GALVESTON, TEXAS, WITH NOTES ON SPECIES IDENTIFICATION [1]

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ABSTRACT

Postlarvae of the genus *Penaeus* were collected at the entrance to Galveston Bay, Tex., over a 4-year period and along Galveston Island's beach during a 1-year period. Postlarval brown shrimp, *P. aztecus,* and white shrimp, *P. setiferus,* were the predominant penaeids caught. Morphological characters, seasonal size differences, and occurrence of juveniles in adjacent nursery areas were used to identify these species. Seasonal occurrence, size distribution, and measures of relative abundance are given for postlarvae of the two species. The uniformity in size of postlarvae from collections along the beach and at the bay entrance indicated that small shrimp do not grow much when they are along the beach.

Shrimp are the most valuable marine fishery resource of the Gulf of Mexico, where commercial landings annually exceed 170 million pounds and are valued at nearly $60 million. Many aspects of the biology and early life history of these crustaceans have been examined; however, the factors causing fluctuations in their abundance must be better defined before optimum management of the shrimp fishery can be realized.

The early life histories of commercially important species of the genus *Penaeus* inhabiting the northwestern Gulf of Mexico are similar. Each spawns in offshore waters, where the planktonic larvae hatch after several hours. During ensuing weeks, the larvae pass through a series of metamorphoses and reach near-shore areas as postlarvae. The young shrimp grow rapidly after moving into estuarine nursery areas, and return to offshore waters to complete their life cycle.

As Bearden (1961) has pointed out, the postlarvae that reach inshore waters represent the success of the spawning season and, after several months of growth, will make up the bulk of the commercial shrimp catch for a given year. Baxter (1963) has shown that systematic sampling of postlarvae entering the major nursery areas can provide an index that is useful for predicting the subsequent abundance of juvenile and adult shrimp on inshore and offshore fishing grounds.

The objectives of this report are to describe trends in the seasonal abundance and size composition of commercial shrimp postlarvae near Galveston Island, and to evaluate the use of seasonal differences in their body lengths as an aid in identifying the various species. Also examined is the question: Do young shrimp use the surf zone as a nursery area? The results of this 4-year study form a basis for current research on the biology and dynamics of the postlarval phase of commercial shrimp populations in the Gulf of Mexico.

SAMPLING PROCEDURE

Studies of postlarval shrimp began as part of a developing investigation of the life history of penaeid shrimp outlined in detail by Kutkuhn (1963). Knowing that shrimp reach shore as postlarvae and

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enter nursery areas through tidal passes, we established a sampling station at the entrance to Galveston Bay in November 1959. Additional stations along Galveston Island's Gulf beach were added later.

GALVESTON ENTRANCE

The initial sampling site was on the south side of the entrance to Galveston Bay (station A, fig. 1),

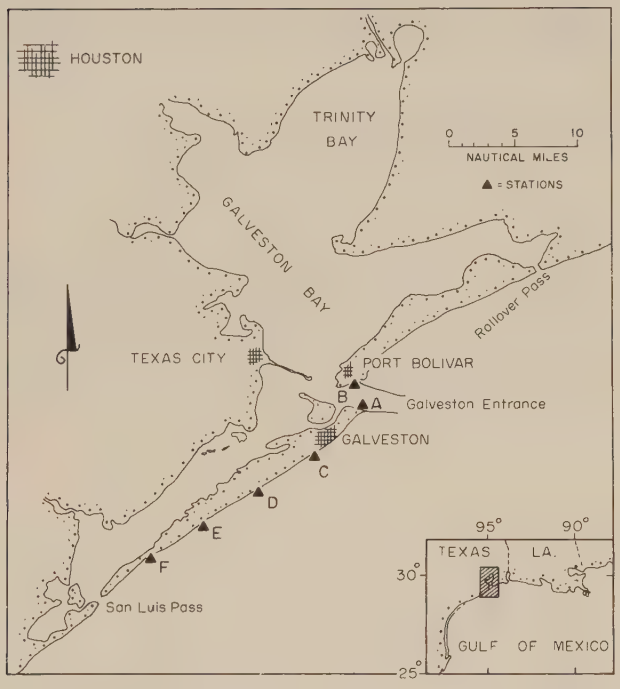

FIGURE 1.—Galveston Island and environs, showing sampling stations.

where we collected postlarval shrimp twice each week. This location was not suitable as a sampling station after Hurricane Carla in September 1961. Thereafter, semiweekly samples were obtained from station B, near the base of the north jetty. Bottom materials at both stations consisted of well-compacted sand.

Collections of postlarvae were made with a 5-foot, hand-drawn beam trawl fitted with a plankton net at its cod end (Renfro, 1963). The wings of the trawl consisted of nylon netting having 50 holes per square centimeter. We believe that escapement of postlarval shrimp was negligible, because most collections contained an abundance of organisms more minute than the smallest postlarvae captured. To test whether or not large shrimp were evading the small beam trawl we towed a fine-mesh, 20-foot seine on several occasions. A standard procedure was followed during each collection. One end of a 150-foot line was tied to a stake driven into the sand at the water's edge. The collector held the free end of this line in one hand and the bridle of the trawl in the other and pulled the gear along the bottom in a semicircular path from the shoreline.

GULF BEACH

Collections of postlarval shrimp were made twice each month between April 1960 and April 1961 at 5-mile intervals along Galveston Island's 25-mile beach (stations C, D, E, and F, fig. 1). The same beam trawl was used at beach stations, but because of the surf, the sampling procedure was altered from that used at stations A and B. The collector waded a measured 75 yards directly offshore, set the gear, and towed it back to shore. Computations of bottom areas sampled were based on distance towed and the dimensions of the net.

At all stations we made meteorological and hydrographic observations. Those that we consider to be pertinent, namely water temperature, salinity, and tidal stage, are listed in appendix tables 1 and 2 along with the numbers of postlarval brown and white shrimp collected on each sampling date.

SEASONAL OCCURRENCE

GALVESTON ENTRANCE

Postlarval brown shrimp, *P. aztecus* Ives, appeared at Galveston Entrance and migrated to the nursery areas within Galveston Bay at about the same time

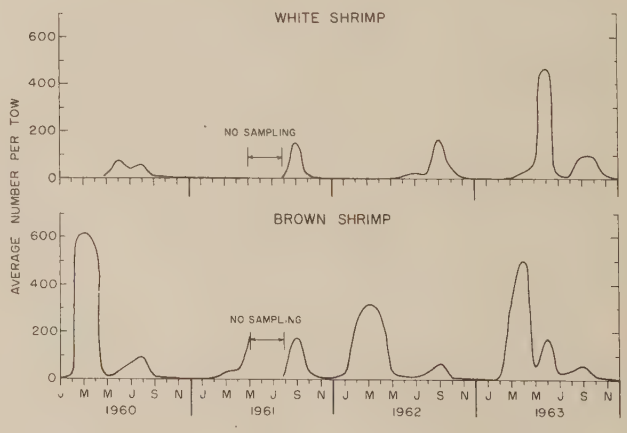

FIGURE 2.—Seasonal abundance of postlarval brown and white shrimp at Galveston Entrance, 1960–63.

during each year of the study (fig. 2). The greatest numbers occurred in the spring; usually peak abundance was reached between mid-March and mid-April. Following the spring peak, comparatively few postlarvae were caught until about mid-June. Thereafter, the number of postlarvae in the collections increased through July and reached a second peak in August or September. In each year, the numbers of brown shrimp postlarvae present at Galveston Entrance diminished rapidly after the second peak and remained low throughout the winter. During 1961, peak abundance appeared to develop in late April and early May, but because sampling was suspended from May 8 to August 11, the actual time of the peak for that year is unknown.

The first postlarval white shrimp, *P. setiferus* (Linnaeus), were taken in early May of each year at Galveston Entrance (fig. 2). Seasonal distribution of postlarval white shrimp suggests that two peaks in abundance may occur each summer and that the relative strength of these peaks is variable.

GALVESTON ISLAND BEACH

Trends in seasonal occurrence of postlarval brown and white shrimp at Galveston Island beach stations were similar to those at Galveston Entrance stations (table 1). Brown shrimp postlarvae were numerous in mid-April 1960, from late June through August, and again during April 1961. In contrast to Galveston Entrance, a few brown shrimp postlarvae were present along the beach during late December and January. In 1961 brown postlarvae did not appear in significant numbers until early March. Postlarval white shrimp were caught in beach samples from mid-May through November 1960 and were most abundant from late June through July. None was taken from December 1960 through April 1961.

Samples of postlarvae were collected along Galveston Island beach to determine if young shrimp use the littoral zone along beaches as nursery areas. Should they use this zone, advanced stages of postlarval shrimp could be expected in collections from beach stations. Agreement as to general size of postlarvae from the beach and from Galveston Entrance (table 2), indicates, however, that postlarvae spend little time in the beach area. Repeated tows with a fine-mesh seine at beach stations caught no shrimp larger than those taken in the beam trawl.

TABLE 1.—*Average monthly densities of postlarval shrimp at Galveston Entrance and Galveston Island beach stations, April 1960–61*

[Figures represent the average number of postlarvae per 100 m.² of bottom in 7 to 12 collections each month]

Month	Brown shrimp postlarvae		White shrimp postlarvae	
	Galveston Entrance	Gulf beach	Galveston Entrance	Gulf beach
1960:				
Apr.	294	52	0	0
May	2	15	6	9
June	23	54	40	52
July	35	234	14	133
Aug.	51	153	29	26
Sept.	0	3	2	39
Oct.	0	3	0	3
Nov.	0	3	0	3
Dec.	1	8	0	0
1961:				
Jan.	0	1	0	0
Feb.	1	1	0	0
Mar.	13	70	0	0
Apr.	72	760	1	0

TABLE 2.—*Mean total lengths of postlarval shrimp collected concurrently along the Galveston Island beach and in Galveston Entrance, 1960–61*

[Figures in parentheses indicate number of specimens measured]

Month	Brown shrimp postlarvae				White shrimp postlarvae			
	Beach		Entrance		Beach		Entrance	
	Mm.		*Mm.*		*Mm.*		*Mm.*	
1960:								
Apr.	11.4	(82)	11.5	(167)				
May	10.4	(52)	10.5	(34)	6.3	(47)	6.4	(51)
June	8.9	(113)	8.8	(101)	5.9	(115)	6.5	(149)
July	8.7	(181)	8.4	(155)	7.2	(186)	6.3	(129)
Aug.	8.6	(241)	8.5	(146)	6.7	(177)	6.3	(153)
Sept.	9.5	(25)	10.0	(10)	7.5	(77)	7.1	(35)
Oct.	10.1	(27)	11.0	(4)	6.8	(24)	7.2	(10)
Nov.	10.9	(23)	11.2	(6)	7.5	(23)	7.5	(8)
Dec.	11.9	(59)						
1961:								
Jan.	11.7	(6)						
Feb.	11.0	(11)	12.0	(6)				
Mar.	11.6	(165)	11.6	(86)				
Apr.	11.3	(200)	11.6	(112)				

IDENTIFICATION AND SEASONAL SIZE DISTRIBUTION

Of the three commercially important species of the genus *Penaeus* in the northern Gulf of Mexico, the pink shrimp, *P. duorarum*, is the least abundant. Small numbers of adult pink shrimp are commonly caught off Galveston Island (15–20 fathoms), but landing data compiled by the Bureau of Commercial Fisheries Branch of Statistics[3] included no pink shrimp in landings of 3.7 million pounds taken from Galveston Bay during 1960–63. A few pink shrimp, however, may have been landed and reported as

[3] "Gulf Coast Shrimp Catch by Area, Depth, Variety, and Size," Annual Summaries, 1960–63.

brown shrimp. Of about 47,000 juvenile shrimp examined from Galveston Bay bait landings between January 1960 and December 1963, only 17 (less than 0.04 percent) were pink shrimp. In earlier work, the second author (1958–59) found no pink shrimp among more than 10,000 juvenile penaeid shrimp taken from upper Galveston Bay. Although postlarval pink shrimp obviously occur in the Galveston area they evidently are scarce; all postlarvae we caught were classified as brown or white shrimp.

MORPHOLOGY

No single criterion is sufficient to distinguish brown and white shrimp postlarvae, but they can be separated by taking into account various morphometric characters, relative size, and seasonal occurrence as juveniles in the estuary. Morphological and morphometric differences between postlarval brown and white shrimp provided by Pearson (1939) and Williams (1959) are sufficient to separate these species during most seasons. Williams, working with shrimp from North Carolina, developed a provisional key to early postlarvae. He stated that the tip of the rostrum and the extended third pereiopod on postlarval white shrimp do not extend to the distal edge of the eye. Conversely, in the brown shrimp, both the tip of the rostrum and extended third pereiopod reach to or beyond the edge of the eye. In postlarvae from the Galveston area, these characteristics suffice only to separate postlarval white and brown shrimp with a total length of 10 mm. or less, whereas Williams was able to use them in North Carolina for separating postlarvae up to 12 mm. total length.

OCCURRENCE ON GALVESTON BAY NURSERY GROUNDS

According to our records, brown shrimp are the only postlarval *Penaeus* that enter Galveston Bay during the first 4 months of the year. This observation agrees with findings from several previous studies conducted in the bay. Renfro (1959) found only brown shrimp postlarvae and juveniles (17 mm. and above) in upper Galveston Bay during April and May 1959. Gunter (1960) also found brown shrimp to be the only species at the juvenile stage present in Galveston Bay during April and May 1960. Later reports by biologists of the Texas Game and Fish Commission corroborate the observations of Renfro and Gunter (Pullen, 1962).

By June, advanced postlarval and early juvenile white shrimp (18–28 mm.) become abundant in Galveston Bay, and both brown and white shrimp are present throughout the summer (Gunter, 1960). Additional evidence regarding the identity of the winter and early spring postlarvae was provided in 1960 when 1,200 postlarvae, taken on April 12 at Galveston Entrance, were brought into the laboratory to be reared. All that grew to identifiable size (150) were brown shrimp.

SEASONAL SIZE DISTRIBUTION

The size of postlarvae caught at the entrance to Galveston Bay provides a strong clue to species identity during some seasons (fig. 3). During the winter, the total length of brown shrimp postlarvae ranged from 10 to 14 mm. and averaged 12 mm. (fig. 3). Beginning in May of each year, a second group of much smaller (6.0 to 8.0 mm.) postlarvae appeared in the samples. These shrimp possessed the external morphological characteristics of postlarval white shrimp described by Pearson (1939) and Williams (1959). By late June the length distributions of the two groups of postlarvae began to overlap. The modes of the length distribution of brown postlarvae decreased, possibly because adult brown shrimp were spawning near shore in spring and summer, or because warm water temperatures increased the developmental rates of larvae. During the same period, some white shrimp postlarvae as long as 10.5 mm. entered the estuary. Most of the larger postlarvae, however, exhibited the characteristics ascribed to brown shrimp by Williams (1959). The overlap in length distributions persisted throughout the summer, but the mean length of brown shrimp postlarvae always exceeded that of white shrimp in the same samples (fig. 3). In the latter part of each year, the modal length of brown shrimp postlarvae increased, and by October in some years the overlap in length distributions had ended.

Postlarvae of brown and white shrimp caught at beach stations and at Galveston Entrance were of similar sizes (table 2). The total length of postlarval brown shrimp ranged from 8.5 to 12.0 mm. (mean, 11.5 mm.). White shrimp ranged from 5.0 to 9.5 mm. (mean, 7.0 mm.). No significant difference existed among the mean lengths of postlarvae taken at the various beach stations on the same day.

SUMMARY

Collections of penaeid postlarvae were obtained semiweekly at Galveston Entrance over a 4-year

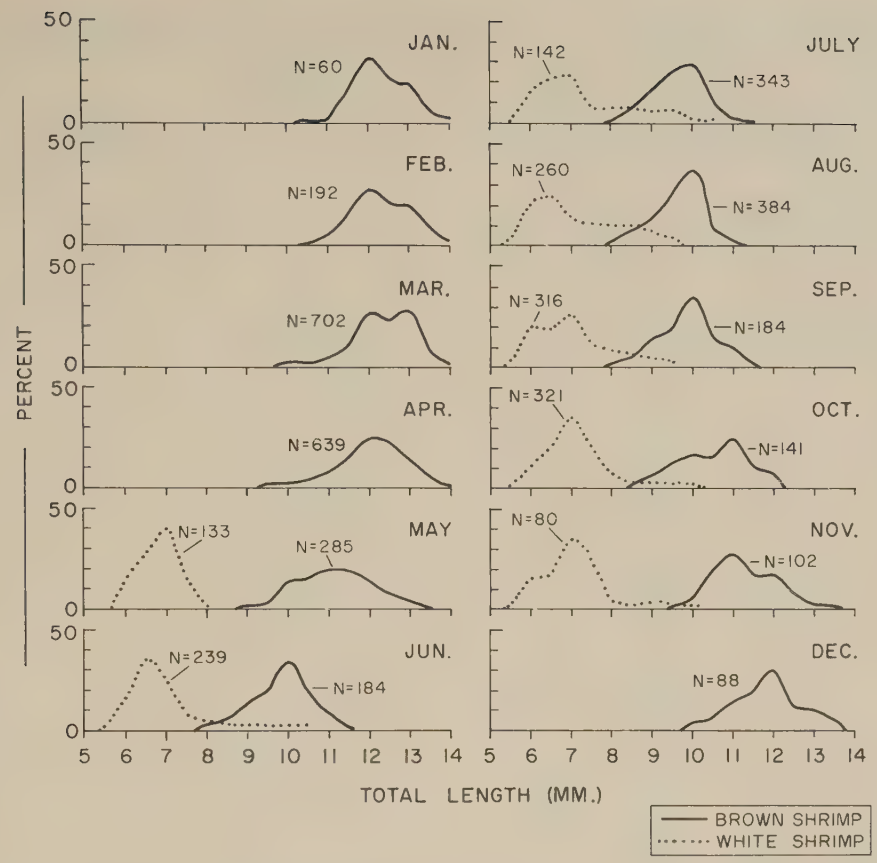

FIGURE 3.—Seasonal size distribution of postlarval brown and white shrimp at Galveston Entrance, 1960–63. (N indicates sample size.)

period and twice each month at four stations along Galveston Island's Gulf beach for 1 year.

Postlarval brown shrimp were collected at Galveston Entrance from February until mid-December of each year. At Galveston beach stations, they were found throughout the year but in smaller numbers during the winter. Numbers of brown shrimp postlarvae reached an annual peak between mid-March and mid-April.

Postlarval white shrimp were first caught at Galveston Entrance and along the beach in May and were most abundant through the summer.

Postlarvae of brown and white shrimp were separated by morphometric characters and by the seasonal occurrence of each species in the adjacent estuary. The brown shrimp was the only *Penaeus* species at the postlarval stage present along the Galveston Island beach and at the entrance of Galveston Bay from December through April. All individuals were relatively large (11 mm. or longer) during this period. After April, their average size decreased, remained relatively small throughout the summer, and then increased again in the fall. White shrimp postlarvae first appeared in May at lengths much shorter than those of brown postlarvae in the same collections; the total lengths of the majority ranged from 6.0 to 8.0 mm. During the summer, the length distributions of postlarvae of brown and white shrimp overlap in the 8- to 10-mm. length range. The two species at this stage of development may, however, be separated by the morphological characteristics described by Pearson (1939) and Williams (1959). At times, the largest white shrimp postlarvae in a sample were longer than the smallest postlarvae of brown shrimp, but the mean lengths of the white postlarvae were always less than those of the brown postlarvae.

The similarity of mean lengths of postlarvae collected along the beach and at Galveston Entrance suggests that significant growth does not occur along the beaches and that the surf zone is not an important nursery area for small shrimp.

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APPENDIX

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1959:						
Nov. 9	1000	0	0			
16	1330	0	0			
Dec. 11	1500	0	0			
18		0	0			
21		0	0			
31		0	0			

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1960:						
Jan. 8		1	0			
13	1530	4	0	15.5	25.3	HWS
15	1100	0	0	14.9	25.3	F
19	1400	0	0	9.8	9.4	E
22	0900	12	0	9.0	23.9	F
25	1100	1	0	10.2	26.0	F
28	1115	1	0	12.5	18.3	F
Feb. 1	1300	1	0	12.2	28.4	
5	1100	0	0	10.2	14.0	F
9	0900	2	0	15.0	31.2	
11	0930	0	0	13.0	27.3	E
16	1100	3	0		16.9	
18	1415	3	0	12.5	12.1	E
24	1000	2	0	10.0	23.6	F
25	1500	2	0	12.0		F
Mar. 1	1345	0	0	10.0	28.6	F
3	1405	0	0	10.5	11.1	E
7	1620	6	0	10.0	26.2	F
11	1330	53	0	13.0	15.9	E
15	1400	39	0	15.0	25.4	
18	1420	72	0	14.2	23.2	E
22	1400	39	0	18.5	28.9	F
28	1100	4,710	0	20.8	26.2	
Apr. 1	1120	3,680	0	19.5	26.9	F
5	1045	86	0	18.2	16.1	F
8	0830	5	0	18.5	25.7	LWS
12	1330	1,000	0	21.0	30.1	F
15	0900	100	0	23.5	28.2	F
19	1115	9	0	22.2	24.1	F
21	1330	50	0	26.0	24.0	HWS
26	1515	56	0	27.0	24.0	F
29	1330	3	0	24.0	23.8	E
May 3	0830	0	0	22.0	22.2	F
6	1400	4	0	24.0	23.0	F
10	0900	6	4	22.2	24.2	E
13	1330	1	1	24.2	29.0	F
17	0845	2	2	24.8	30.5	F
20	0900	9	12	25.6	29.5	F
23	0830	7	82	25.4	27.8	E
26	1545	5	6	29.0	26.9	E
31	1500	0	1	31.2		HWS
June 3	1400	0	12	30.7	27.2	LWS
6	1030	0	23	29.0	29.3	F
9	1030	0	0	29.5	32.5	F
14	0830	0	8	28.0	31.2	F
17	0900	167	428	28.4	31.8	E
21	0930	1	6	29.0	32.7	F
24	1515	65	25	28.2	32.5	F
27	1400	108	60	30.0	31.1	F
30	0900	38	98	30.0	26.8	F
July 5	1500	74	148	31.9	31.4	LWS
8	1445	4	1	33.2	25.8	F
12	0930	61	28	30.0	29.4	E
15	1300	30	6	32.0	25.8	E
19		18	71	29.0	29.6	F
21	1330	73	35	32.0	31.3	F
25	0940	241	21	30.0	35.5	F
29	1410	8	1	34.0	28.0	E
Aug. 1		148	117	29.5	35.6	E
5	1345	21	27	32.0	36.1	F
9	1330	16	24	33.3	34.2	F
12	1430	0	4	29.5	26.3	E
15	1330	257	202	31.0	33.3	E
19	1600	1	2	30.5	27.1	E
22	1000	81	20	28.0	27.8	E
25	0915	306	77	29.5	28.8	LWS
29	1220	8	3	29.0		F
Sept. 2	1130	4	9	31.4	26.5	F
6	1400	3	10	32.0	24.6	F
9	1010	0	3	30.1	23.2	E
12	0900	0	1	27.0	25.9	
16	0930	0	0	27.0	21.3	E
20	0950	1	4	29.0	27.0	E

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	*°C.*	o/oo	
1960:—Continued						
Sept. 23	1310	1	2	32.0	27.8	LWS
27	1400	2	5	28.0	24.1	E
30	1615	0	0	30.0	26.5	LWS
Oct. 3	1400	0	0	28.0	28.6	F
7	1100	2	3	27.2	24.6	E
11	1400	0	1	30.0	26.7	E
14	1400	0	2	25.8	28.6	F
17	0845	2	3	25.0	27.0	F
20	0930	0	0	21.0	16.3	E
25	0900	0	0	23.5	27.3	F
28	1415	0	1	27.0	25.5	E
31	1430	0	1	21.3	17.1	E
Nov. 3	1415	1	5	24.0	20.0	F
7	1430	0	0	21.0	22.9	F
10	1600	0	0	12.5	17.9	E
15	1145	1	2	24.0	26.2	F
18	1415	0	0	18.5	26.9	F
21	1630	0	0	18.0	24.9	F
25	1430	1	0	20.0	11.2	E
28	1545	3	1	22.5	24.5	F
Dec. 2	1545	0	0	16.0	27.8	F
6	1530	0	0	19.0	27.1	F
9	1500	1	0	15.5	29.5	F
13	1545	0	0	13.5	31.0	E
16	1445	6	0	13.0	19.2	E
19	1440	0	0	12.0	-------	E
22	1500	0	0	12.2	25.4	E
27	1100	0	0	13.0	19.4	F
29	1145	0	0	12.5	11.1	F
1961						
Jan. 3	1330	0	0	11.8	14.4	E
6	1135	0	0	12.2	24.9	F
10	1530	0	0	13.0	-------	E
13	1405	0	0	12.4	8.3	E
16	1115	0	0	12.5	15.2	E
20	1500	0	0	14.8	7.8	E
25	1410	0	0	10.2	26.8	F
27	1340	0	0	8.0	12.7	E
30	1340	0	0	11.8	11.9	E
Feb. 3	1420	0	0	13.0	13.8	E
7	1430	0	0	11.0	10.8	E
10	1415	0	0	13.0	24.4	F
17	1405	4	0	19.2	28.6	E
21	1420	0	0	15.0	7.6	E
24	1100	0	0	17.0	8.9	E
27	1115	2	0	15.0	10.9	F
Mar. 3	1350	6	0	19.0	30.2	E
6	1510	5	0	19.4	21.8	E
10	1520	2	0	17.8	26.7	E
14	1430	1	0	19.2	26.7	F
17	1400	97	0	20.5	26.7	E
21	1520	28	0	19.7	25.9	E
27	1440	2	0	27.4	25.8	E
31	1040	42	0	20.1	18.2	E
Apr. 5	0845	6	0	19.2	25.3	F
7	1515	12	0	19.5	30.9	E
11	1045	4	0	19.1	29.2	F
17	1555	209	0	20.0	27.8	E
21	1600	10	0	23.0	29.4	E
25	1600	3	0	24.0	25.6	F
28	1550	2	0	24.1	15.0	E
May 2	1355	51	0	25.8	16.6	E
8	1500	889	10	26.9	19.1	E
		—SAMPLING INTERRUPTED—				
Aug. 11	1720	0	0	31.7	30.5	E
15	1410	5	15	33.8	30.3	E
17	0845	6	11	29.8	28.4	E
21	1400	24	10	31.5	20.6	E
24	0915	54	6	29.8	24.6	E
28	1400	8	0	29.8	22.2	F

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	*°C.*	o/oo	
1961:—Continued						
Sept. 1	1415	520	544	30.9	24.3	E
6	1415	65	44	33.9	22.3	E
		—HURRICANE CARLA—				
25	1200	5	0	32.0	17.2	F
27	1510	4	0	34.0	17.2	F
Oct. 2	0925	2	1	29.0	18.1	F
5	0900	6	3	20.0	27.8	F
10	1005	32	1	29.0	27.3	E
12	1400	5	0	30.2	24.8	E
16	1545	61	74	24.5	27.4	E
19	1520	6	7	27.0	25.7	E
23	0925	0	0	23.5	24.7	E
25	0905	2	0	24.9	26.3	E
27	0920	144	77	20.5	28.5	E
30	1425	11	3	30.0	29.1	E
Nov. 3	1345	9	4	19.5	27.0	F
6	1520	3	0	12.0	24.0	F
9	0910	45	0	13.0	24.7	E
14	0940	13	1	19.0	23.5	E
16	0945	0	0	17.0	15.0	E
21	0940	1	0	17.5	28.7	F
24	1405	0	0	19.0	28.7	F
27	1020	4	0	21.5	27.5	E
30	0945	0	0	12.0	28.4	LWS
Dec. 5	0930	21	0	20.0	27.5	E
8	1430	0	0	16.0	27.0	F
11	0920	11	0	20.5	25.6	E
14	0920	0	0	8.5	23.1	HWS
19	0925	2	0	13.5	24.4	E
22	1400	1	0	18.0	26.3	E
26	0945	9	0	13.5	27.9	E
29	0920	0	0	10.0	24.4	E
1962:						
Jan. 2	1410	0	0	15.0	27.5	LWS
4	0925	12	0	16.0	31.2	E
9	0925	224	0	12.0	31.0	E
12	0905	5	0	−2.0	30.5	F
15	0905	0	0	6.0	29.9	E
17	1400	0	0	9.0	29.8	F
23	1410	0	0	9.0	27.7	E
26	1045	0	0	15.0	27.2	F
29	0900	0	0	10.0	25.7	LWS
Feb. 1	1550	1	0	14.0	26.5	F
6	0845	73	0	9.0	31.4	E
9	1400	34	0	22.0	29.6	E
12	1030	196	0	19.0	26.3	F
15	1400	48	0	21.0	27.6	F
19	0925	222	0	15.0	27.6	E
23	1340	53	0	22.0	22.3	E
26	0900	1,220	0	22.0	21.7	F
Mar. 1	1525	0	0	5.5	23.0	F
6	1030	40	0	12.0	23.3	E
9	1415	368	0	24.0	24.7	E
12	1100	66	0	17.5	25.5	F
16	1415	8	0	17.5	19.5	F
20	0925	506	0	19.5	26.9	LWS
23	1440	626	0	20.5	26.7	F
26	1035	140	0	19.0	22.3	F
29	1420	75	0	24.0	28.9	F
Apr. 4	0925	1,682	0	16.0	27.0	E
6	1445	234	0	23.0	25.5	E
9	0900	24	0	21.0	24.4	F
12	1445	135	0	24.0	25.3	E
17	0925	192	0	20.5	24.9	E
20	1430	44	0	27.5	24.4	F
23	0905	103	0	24.0	25.2	F
26	1400	3	0	26.0	24.6	F
May 1	1000	4	0	26.0	23.3	E
3	1425	250	0	24.0	18.0	F
7	0910	23	0	24.1	17.7	F
10	0925	7	0	25.0	23.6	F

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrogfaphic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1962:—Continued						
May 15	0925	2	0	26.0	31.7	HWS
18	1500	0	0	27.9	24.2	F
21	0915	0	0	27.0	23.8	F
24	1500	0	0	29.0	24.7	F
29	0905	3	1	26.0	18.9	E
June 1	1430	0	2	26.0	15.7	HWS
4	0925	0	6	26.0	14.7	F
8	1510	6	0	31.5	17.9	HWS
12	0950	8	4	29.5	18.6	E
15	1100	0	0	31.5	26.8	HWS
18	0855	32	6	31.0	26.1	F
21	1423	16	28	34.0	24.4	F
26	0945	0	0	30.5	24.6	F
29	1450	6	6	32.0	23.8	E
July 2	0905	11	13	30.0	23.2	F
5	1100	17	15	33.0	19.9	F
10	0905	0	1	32.0	20.0	E
13	1410	0	0	33.0	31.5	E
16	0845	13	61	30.0	29.8	F
19	1445	48	116	34.0	33.6	E
24	0900	0	1	31.0	35.5	F
27	1410	3	4	32.5	37.4	HWS
30	0910	1	5	30.0	33.8	E
Aug. 2	1415	14	4	33.0	34.4	E
8	0900	19	2	31.0	31.4	E
10	1430	4	4	35.0	35.6	E
13	0905	0	0	30.0	34.4	E
16	1400	145	46	32.0	35.8	F
21	0915	16	29	31.0	36.1	E
24	1405	25	31	33.5	35.6	E
27	0925	76	36	29.0	36.1	E
30	1420	6	29	31.0	29.8	F
Sept. 4	0900	15	106	31.0	30.5	E
7	1410	3	10	31.0	28.6	E
10	0925	25	38	30.5	31.0	E
13	1425	2	2	33.0	31.5	F
18	0905	37	78	30.0	28.7	E
21	1505	11	42	27.0	26.8	E
24	1045	2	7	28.0	25.3	LWS
27	1410	367	1,227	26.0	27.0	F
Oct. 2	1500	24	96	29.0	27.8	F
5	1430	0	6	27.0	26.9	E
8	0920	0	17	29.5	27.0	E
11	1420	0	0	31.0	28.7	F
16	0910	0	1	29.0	30.1	E
19	1440	2	11	29.0	29.8	E
22	0845	6	150	23.0	28.8	LWS
25	1410	4	29	22.0	30.2	F
30	0905	12	46	18.0	26.5	E
Nov. 2	1505	6	13	22.0	29.2	E
5	0845	0	0	17.0	29.1	E
8	1405	1	4	20.0	29.3	E
13	0930	2	0	14.0	30.8	E
16	1445	6	0	22.0	30.9	E
19	0915	0	0	12.0	31.0	F
23	0900	0	0	16.0	29.7	E
26	0905	1	0	18.5	29.9	E
29	1450	0	0	11.0	22.9	F
Dec. 3	0845	13	1	16.5	29.1	E
6	1405	0	0	16.5	20.8	F
11	0915	0	0	16.0	30.6	E
14	1315	0	0	12.0	32.4	LWS
17	0915	0	0	9.0	31.5	F
20	1410	39	0	20.0	31.8	F
26	0905	0	0	11.0	26.3	E
28	1600	0	0	13.0	22.7	F
31	1035	0	0	11.5	28.1	E
1963						
Jan. 4	1445	0	0	15.0	29.1	F
8	0930	1	0	11.0	23.2	E
11	1430	0	0	16.0	31.3	F
14	0845	0	0	0.0	32.4	E

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1963:—Continued						
Jan. 17	1310	0	0	9.0	29.5	F
22	0900	0	0	9.0	24.9	E
25	1430	0	0	7.0	28.5	F
28	0935	0	0	1.0	27.9	E
31	1410	0	0	15.0	25.9	F
Feb. 5	1115	0	0	12.0	29.8	E
7	1435	0	0	16.0	29.6	F
11	0940	0	0	9.0	31.5	E
14	1430	0	0	11.0	25.8	E
19	0935	0	0	8.0	27.2	E
21	1410	0	0	16.0	29.6	F
25	0930	0	0	11.0	28.7	E
28	1415	0	0	15.0	29.7	F
Mar. 5	0920	441	0	14.5	30.4	E
8	1415	16	0	16.0	30.6	F
11	0925	288	0	17.0	30.4	E
14	1400	21	0	18.0	29.0	F
19	0850	280	0	21.0	29.2	HWS
22	1425	286	0	15.0	27.4	E
25	0840	986	0	20.0	26.9	F
28	1350	114	0	27.0	25.9	HWS
Apr. 2	0958	360	0	22.5	27.6	F
5	1146	3,521	0	20.0	27.6	F
8	0925	147	0	21.0	27.6	LWS
11	1415	54	0	28.0	30.6	F
16	0910	167	0	23.8	33.0	F
19	1415	44	0	27.0	32.0	F
22	0910	103	0	25.0	28.0	F
25	1410	93	0	29.0	21.0	E
30	0855	41	3	24.0	21.6	F
May 3	1410	68	5	30.0	20.5	F
6	0910	181	272	25.0	21.7	E
9	1400	71	9	27.0	24.2	F
14	0910	10	0	26.0	28.8	F
17	1410	16	1	29.0	29.0	F
20	0950	17	2	28.0	31.3	E
23	1435	134	70	27.0	34.5	F
28	0915	29	26	27.5	32.3	F
31	1405	28	115	32.0	33.2	F
June 3	0910	381	3,407	34.0	34.8	E
6	1415	5	117	32.0	32.6	E
11	0915	6	19	30.0	30.8	F
15	0915	38	21	28.0	32.9	F
17	1410	7	18	35.0	32.3	F
20	1440	24	10	31.0	33.1	F
25	0915	882	548	29.0	29.9	F
28	1410	211	4	35.0	27.1	F
July 1	0910	16	0	30.0	31.2	F
5	1415	62	9	32.5	31.3	HWS
9	0910	59	29	30.0	31.1	E
12	1415	23	2	31.0	34.3	F
15	0910	33	0	29.0	31.8	F
18	1420	11	2	33.0	34.9	E
23	0910	32	0	31.0	33.6	F
26	1420	23	3	26.0	29.1	LWS
29	0935	14	6	31.0	36.1	E
Aug. 1	1415	7	5	34.0	35.2	E
6	0915	51	21	31.0	34.6	E
9	1415	94	30	33.5	36.5	LWS
12	0915	19	36	29.0	35.0	E
15	1430	27	26	29.5	35.2	E
20	0910	48	12	30.0	35.9	F
23	1415	93	38	35.0	36.9	E
26	0910	4	0	30.0	36.4	E
29	1430	10	5	34.0	37.1	E
Sept. 3	0930	41	28	30.0	37.6	F
6	1430	10	14	29.5	33.3	LWS
9	0910	1	18	30.0	37.1	HWS
12	1410	6	35	32.0	36.7	E
18	0910	24	264	24.0	28.2	F
20	1415	206	132	29.0	27.7	HWS
23	0935	60	94	25.0	27.4	E
26	1420	68	167	26.0	24.9	LWS

See footnote at end of table.

TABLE A-1.—*Numbers of postlarval shrimp collected and associated hydrographic observations, Galveston Entrance, 1959–63*—Continued

Date	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
		P. aztecus	*P. setiferus*			
		Number	*Number*	°C.	o/oo	
1963:—Continued						
Oct. 1	0910	54	177	21.0	29.3	E
4	1415	4	2	24.0	29.6	LWS
7	0910	19	141	26.0	29.5	E
10	1415	0	47	30.0	30.5	E
15	0910	6	76	26.0	31.4	E
18	1405	14	44	26.5	32.6	F
21	0915	2	14	24.0	31.7	E
24	1415	2	14	26.0	31.8	E
29	0915	10	309	21.0	31.4	HWS
Nov. 1	1505	0	0	19.5	30.7	F
4	0925	4	19	21.0	30.8	E
7	1430	0	0	25.0	30.6	E
12	0925	3	39	18.0	30.0	E
15	1410	0	0	----------	30.3	F
18	1505	17	15	26.0	31.3	F
26	1100	0	0	17.0	30.7	F
Dec. 2	1420	0	0	20.0	30.4	E
5	1415	0	0	17.0	32.5	E
10	0950	0	0	15.0	32.8	F
13	1410	0	0	9.0	29.9	F
16	0930	0	0	5.0	31.0	E
19	1430	0	0	9.0	30.3	E
24	1430	0	0	10.0	29.9	E
27	1515	0	0	18.0	31.1	F
30	1005	0	0	10.0	32.8	E

[1] F = Flood; E = Ebb; HWS = High-water slack; LWS = Low-water slack.

TABLE A-2.—*Numbers of postlarval shrimp and associated hydrographic observations, Galveston Island beach stations, 1960–61*

Date	Station	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
			P. aztecus	*P. setiferus*			
			Number	*Number*	°C.	o/oo	
1960:							
Apr. 14	C	----	----------	----------	----------	----------	----
	D	1200	18	0	21.2	29.8	HWS
	E	1245	137	0	21.5	30.2	HWS
	F	1345	161	0	22.2	30.7	E
27	C	0900	1	0	24.2	23.9	F
	D	0940	3	0	24.7	24.0	F
	E	1030	5	0	25.2	24.2	F
	F	1115	5	0	25.5	23.3	F
May 11	C	1045	0	0	23.2	30.1	LWS
	D	1130	3	0	23.6	30.3	LWS
	E	1230	4	0	23.2	30.8	F
	F	1330	3	1	23.0	31.0	F
25	C	0830	1	4	26.3	29.2	E
	D	0915	11	3	26.8	29.7	E
	E	1000	89	50	27.0	29.8	E
	F	1045	5	14	27.0	29.7	E
June 8	C	0900	2	9	28.0	32.7	F
	D	0945	3	3	29.0	33.1	F
	E	1030	6	2	29.1	33.5	F
	F	1100	2	1	29.0	33.9	F
22	C	0840	191	64	29.6	32.9	E
	D	0940	51	107	30.0	32.9	E
	E	1020	113	122	30.1	33.1	F
	F	1100	28	73	30.8	33.1	F

See footnote at end of table.

TABLE A-2.—*Numbers of postlarval shrimp and associated hydrographic observations, Galveston Island beach stations, 1960–61*—Continued

Date	Station	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
			P. aztecus	*P. setiferus*			
			Number	*Number*	°C.	o/oo	
1960:—Continued							
July 6	C	0930	6	11	29.8	31.5	LWS
	D	1000	135	90	30.8	31.9	F
	E	1030	112	168	30.6	31.3	F
	F	1200	125	62	33.0	31.7	F
20	C	0840	39	36	29.4	33.4	E
	D	0920	432	288	29.3	33.4	HWS
	E	1045	392	54	30.0	33.9	E
	F	1200	390	260	30.4	33.3	F
Aug. 3	C	0830	59	63	29.7	36.1	F
	D	0930	97	24	29.8	36.0	F
	E	1000	168	15	30.0	35.9	F
	F	1120	1	0	30.5	35.9	F
16	C	0830	10	10	28.5	--------	F
	D	0910	166	14	28.9	32.4	F
	E	1000	897	78	29.2	32.1	F
	F	1130	160	51	30.0	32.2	E
31	C	0840	10	0	29.0	27.5	F
	D	0930	20	13	29.0	29.4	F
	E	1045	28	14	30.2	--------	F
	F	1205	65	12	31.2	--------	E
Sept. 15	C	0840	6	74	27.8	25.9	F
	D	0935	8	189	28.0	25.5	E
	E	1110	3	12	28.5	25.4	E
	F	1305	2	10	31.3	25.7	E
Sept. 28	C	0845	0	2	24.0	28.1	E
	D	0930	1	1	24.0	28.2	E
	E	1200	0	0	26.0	28.6	E
	F	1040	5	2	25.0	28.6	E
Oct. 12	C	0840	0	0	27.0	28.1	E
	D	0930	1	2	27.4	28.8	E
	E	1030	1	7	27.8	28.9	E
	F	1110	6	5	28.0	29.2	E
26	C	0845	3	4	23.8	27.3	E
	D	0945	2	1	24.4	27.6	E
	E	1040	6	1	24.2	27.2	E
	F	1150	8	4	23.8	26.5	E
Nov. 9	C	1330	1	0	21.3	26.9	E
	D	1110	0	0	21.5	27.5	E
	E	1445	1	0	21.8	27.5	E
	F	1520	0	4	22.0	28.8	E
23	C	1320	0	4	19.5	25.5	E
	D	1405	1	1	20.0	27.3	E
	E	1435	14	11	19.5	25.7	E
	F	1540	6	3	20.0	25.4	F
Dec. 8	C	1405	17	0	17.0	28.2	F
	D	1435	8	0	16.5	28.1	F
	E	1515	18	0	17.0	28.6	F
	F	1600	15	0	16.5	--------	F
Dec. 21	C	1355	1	0	10.2	29.3	E
	D	1430	0	0	10.2	29.1	E
	E	1515	0	0	11.0	28.7	E
	F	1545	0	0	12.0	--------	E
1961:							
Jan. 4	C	0930	0	0	10.8	27.3	E
	D	1015	0	0	10.9	26.5	E
	E	1100	1	0	11.7	27.3	E
	F	1130	0	0	11.6	26.8	E
18	C	0930	0	0	14.5	27.9	E
	D	1030	3	0	16.0	32.7	F
	E	1115	1	0	16.5	32.9	F
	F	1200	1	0	16.0	32.4	F
Feb. 1	C	1330	0	0	13.0	26.5	E
	D	1420	0	0	13.0	24.6	E
	E	1440	0	0	14.0	24.9	F
	F	1530	0	0	14.0	24.9	F

See footnote at end of table.

TABLE A-2.—*Numbers of postlarval shrimp and associated hydrographic observations, Galveston Island beach stations, 1960–61*

Date	Station	Time	Postlarvae per standard tow		Water temperature	Salinity	Tidal stage[1]
			P. aztecus	*P. setiferus*			
			Number	*Number*	°C.	o/oo	
1961:—Continued							
Feb. 20	C	1320	0	0	17.4	26.9	F
	D	1400	2	0	16.9	27.4	F
	E	1435	7	0	17.2	26.9	F
	F	1500	2	0	16.8	26.8	F
Mar. 8	C	1335	14	0	18.0	28.8	E
	D	1415	50	0	16.7	28.8	E
	E	1445	18	0	17.5	29.1	E
	F	1510	138	0	17.9	29.3	E
Mar. 23	C	0900	8	0	17.9	27.2	F
	D	0937	145	0	18.4	27.2	F
	E	1020	72	0	19.0	27.4	F
	F	1037	69	0	19.8	27.4	F
Apr. 5	C	1315	141	0	20.0	29.2	F
	D	1355	217	0	19.7	27.7	F
	E	1425	1,040	0	20.0	30.7	F
	F	1455	2,662	0	----------	33.6	E
20	C	1335	173	0	24.2	29.1	E
	D	1410	254	0	24.0	29.6	E
	E	1430	196	0	23.6	30.4	E
	F	1515	850	0	24.0	31.0	E

[1] F = Flood; F = Ebb; HWS = High-water slack; LWS = Low-water slack.

CODIUM ENTERS MAINE WATERS

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An exotic species of marine algae, *Codium fragile* (Sur.) subsp. *tomentosoides* (Hariot) (fig. 1) was found growing in Boothbay Harbor, Maine, near the Bureau of Commercial Fisheries Biological Laboratory on July 17, 1964. Although the species has been established in the Long Island (N.Y.) and Cape Cod regions for several years, this is its first record from the Atlantic coast north of Cape Cod. In many oyster producing areas, *Codium* grows luxuriantly on the oyster shells and is considered to be a serious pest by the oyster growers.

The specimens from Boothbay Harbor were all collected within 400 m. of the Biological Laboratory in a sheltered cove, and all but one were attached to various objects just below the low tide mark; the single exception was unattached and entangled in some fronds of rockweed (*Ascophyllum nodosum*). Among the substrata to which *Codium* was attached were stones, *Modiolus modiolus* shells, seaweeds, and waterlogged timbers. Because Galtsoff[1] had reported *Codium* from depths down to 12 m., SCUBA divers surveyed the same general area for subtidal specimens. Their survey, as well as littoral surveys in other parts of the harbor, yielded no additional specimens, although more were subsequently found near the site of the original discovery.

Table 1 summarizes the data on all plants collected from July 20, 1964 to August 5, 1965. Gametangia were found on plants only during July and August. Nine specimens bearing gametangia were examined histologically to determine their sex: five bore mostly male, three bore mostly female, and one had about equal numbers of male and female gametangia.

Growth in the Boothbay Harbor area appears to be rapid even during the cold part of the year. For example, plants collected in May 1965 apparently had grown as much as 34 cm. in length since the previous November when they were so small as to be barely visible.

Table 1.—Codium fragile *var.* tomentosoides *collected in the Boothbay Harbor area, 1964–65*

Date collected	Specimens	Length range	Mean length	With gametangia
1964:	*Number*	*Cm.*	*Cm.*	*Number*
July 20	18	9–54	25.6	17
Aug. 11	10	8–20	13.2	7
Sept. 9	7	10–16	13.5	none
Nov. 23	1	20	20.0	Do.
Nov. 24	2	17–20	18.5	Do.
1965:				
May 5	6	11–34	20.3	Do.
July 7	16	3–24	10.6	Do.
Aug. 4	2	13–14	13.5	1
Aug. 5	4	18–43	26.0	4

In the past 60 years, *Codium fragile* appears to have spread widely throughout the world. Silva (1955) presumed its original center of distribution to be the Pacific and Subantarctic regions, perhaps in Japan. It appeared in Holland about 1900 (Van Goor, 1923) and spread to Denmark, Norway, Sweden, England, and France (Silva, 1955). The introduction of *Codium* in Cape Cod was described by Wood (1962), as well as Galtsoff. No certain evidence is available to explain the source of its introduction in Long Island, N.Y., or that of its recent appearance in Maine. One possible explanation of the Maine introduction might be that the

Note.—Approved for publication April 20, 1966.

[1] P. S. Galtsoff in a manuscript on file at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Mass., first called attention to *Codium* on Cape Cod in January 1962.

FIGURE 1.—Two typical specimens of *Codium fragile* subsp. *tomentosoides* collected in Boothbay Harbor, Maine.

FIGURE 2.—Utricles and attached gametangia from a specimen of *Codium fragile* subsp. *tomentosoides*.

plant arrived on oysters (*Crassostrea virginica*) shipped from Long Island to Boothbay Harbor to delay their spawning by holding them in the colder Maine waters. These oysters were customarily inspected, however, both upon arrival and again before return, to prevent the possible introduction of undesirable species. *Codium* in very early stages of development may have been overlooked when the oysters arrived from Long Island, because at the time *Codium* was not one of the undesirable species being checked; nevertheless, the reexamination before returning the oysters should have brought to light the plants at a larger stage of development.

Codium could possibly have been introduced on the hulls of some of the yachts visiting the area. Such an explanation was not favored by Rosenvinge (1920) who believed the spread in Europe to be due to the breaking loose and drifting of plants or to their being transported along with oysters or other shellfish.

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LABORATORY EVALUATION OF RED-TIDE CONTROL AGENTS[1]

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Intense blooms of the dinoflagellate *Gymnodinium breve* Davis that occur at irregular intervals along the west coast of Florida (Feinstein, Ceurvels, Hutton, and Snoek, 1955) may cause extensive mortality of marine organisms. The blooms are popularly known as red tides because of the amber to red discoloration they impart to the water.

The Fish and Wildlife Service initiated studies in 1948 to determine the possibility of artificial means to reduce the occurrence or intensity, or both, of the red tides. Early tests indicated that copper, in concentrations as low as 0.03 p.p.m., is lethal to laboratory cultures of the red-tide organism. Rounsefell and Evans (1958), and Marvin, Lansford, and Wheeler (1961) demonstrated, however, that control by copper was not feasible under field conditions. The copper precipitated from solution after a few days and, consequently, was ineffective for control.

In 1959, scientists of the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Tex., began a systematic evaluation of 4,306 compounds as red-tide toxicants. The initial phase of the study (Marvin and Proctor, 1964) involved testing each compound to determine its toxicity to *G. breve*. The final phase of the study, described here, evaluated some of the more toxic materials in the laboratory. We investigated only the compounds that we determined to be 100-percent lethal to *G. breve* within 24 hours at concentrations of 0.01 p.p.m. or less. A red-tide control agent must also be selectively toxic; it must kill the red-tide organism without harming other species.

The chemicals fulfilling the toxic requirement for red-tide control were tested for selectivity by determining their effects on juvenile forms of marine species living in Galveston Bay and adjacent coastal waters. The selectivity threshold concentration was set arbitrarily at 0.1 p.p.m. Chemicals that killed 50 percent or more of any test organism within 24 hours at or below this concentration were rejected. The five chemicals that passed the selectivity tests, their effects on the test organisms at the threshold concentration, and the species tested are noted in table 1.

[1] Contribution No. 215, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex.
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Table 1.—*Percentage mortality of test organisms held 24 hours at toxicant concentration levels of 0.10 p.p.m.*

Chemical	Species[1]							
	Blue crab (megalops)	Striped mullet	Brown shrimp (postlarval)	Sailfin molly	Marsh periwinkle	Sheepshead minnow	Hermit crab	Atlantic croaker
Carbamic acid, diethyldithio-; tellurium salt	0	0	10	10	0	0	0	0
Carbamic acid, dimethyldithio-; ferric salt	10	0	0	0	0	40	0	0
Disulfide, bis(diethylthiocarbamyl)	0	0	10	0	0	0	0	20
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; bis dimethylamino butyne monosalt	10	0	20	0	10	0	0	0
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; cyclohexylamine mono salt	0	0	0	20	0	20	0	10

[1] Blue crab, *Callinectes sapidus* Rathbun; Striped mullet, *Mugil cephalus* Linnaeus; Brown shrimp, *Penaeus aztecus* Ives; Sailfin molly, *Mollienesia latipinna* LeSueur; Marsh periwinkle, *Littorina irrorata* Say; Sheepshead minnow, *Cyprinodon variegatus* Lacépède; Hermit crab, *Pagurus* spp.; Atlantic croaker, *Micropogon undulatus* (Linnaeus).

TABLE 2.—*Results of six toxicity tests in terms of percentage mortality of* G. breve *after 24 hours exposure*

Chemical	Test numbers for concentration of 0.01 p.p.m.						Test numbers for concentrations of 0.003 p.p.m.					
	1	2	3	4	5	6	1	2	3	4	5	6
Carbamic acid, diethyldithio-; tellurium salt	100	100	100	100	100	100	0	0	0	25	0	0
Carbamic aid, dimethyldithio-; ferric salt	100	100	75	100	100	25	0	0	0	50	0	0
Disulfide, bis(diethylthiocarbamyl)	100	100	75	100	100	0	0	0	0	50	0	0
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; bis dimethylamino butyne mono salt	25	100	50	100	75	25	0	0	0	0	0	0
Sulfide, bis(2-hydroxy-3-bromo-5-chlorophenyl)-; cyclohexylamine mono salt	25	50	25	100	100	0	0	0	0	0	0	0

The selective chemicals were tested to determine their minimum toxic concentration levels to *G. breve*. Each toxicant was tested six times at 0.01 and 0.003 p.p.m. The results, in terms of mortality of *G. breve*, appear in table 2. Variation was considerable among the supposedly replicate sets of four of the chemicals. This suggests that the concentration of these four chemicals was close to the toxic threshold. At or close to the toxic threshold level, a slight variation in the concentration of a toxicant can have a pronounced effect on the mortality of organisms in cultures containing the toxicant.

Only one of the selective toxicants, carbamic acid, diethyldithio-; tellurium salt, consistently met the toxic requirement arbitrarily established for a control agent (R. T. Vanderbilt Co., Inc., 230 Park Avenue, New York City, N.Y. 10017; $2.13 per pound in 100-pound containers). This compound has two shortcomings, however: it killed 10 percent of the test organisms of two species (table 1); and its cost is prohibitive for massive use in the field.

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